

1 **Colony-specific differences in decadal longitudinal body composition of a**
2 **capital-breeding marine top predator**

3
4 Nora Hanson¹, Sophie Smout^{1,2}, Simon Moss¹, Patrick Pomeroy¹

5
6 ¹Sea Mammal Research Unit, University of St Andrews, St Andrews, UK

7 ²Centre for Research into Ecological & Environmental Modelling, University of St
8 Andrews, St Andrews, UK

9 Correspondence: Nora Hanson, Marine Scotland Science, Pitlochry, UK. Email:

10 nora.hanson@gov.scot

11

12

ABSTRACT

13 1. Capital breeding animals such as true seals (*Phocidae*) rely on accumulated
14 body reserves to rear offspring. A mother's body composition at the start of a
15 breeding episode may depend on recent environmental conditions, and sets
16 the resources available for the reproductive episode.

17 2. At two grey seal (*Halichoerus grypus*) breeding colonies with contrasting
18 demographic characteristics, factors influencing individual variation and
19 temporal trends in the body composition (expressed as the lipid to protein
20 mass ratio) of females were examined.

21 3. Maternal reproductive expenditure, and the consequences for mothers and
22 their pups, were investigated.

- 23 4. Variation in postpartum maternal body composition was considerable. Mean
24 values of 27% (\pm 5%) lipid and 18% (\pm 1%) protein were estimated by
25 hydrogen isotope dilution.
- 26 5. Mothers with a high lipid to protein mass ratio expended a higher proportion
27 of lipid resources while conserving protein and weaned heavier pups.
- 28 6. Average maternal postpartum body composition was similar between the two
29 colonies but declined during the study period at one colony where pup
30 production was decreasing and increased at another where pup production
31 was increasing.

32

33 **KEYWORDS:** behaviour, coastal, mammals, physiology, reproduction

34

35

36 1. INTRODUCTION

37 Resource limitation forces long-lived iteroparous animals to trade-off survival,
38 growth and reproduction during their lifetime (e.g. Festa-Bianchet, Gaillard, &
39 Jorgenson, 1998; Ronget et al., 2018; Schick et al., 2013; Sheldon & West,
40 2004). Body composition provides a measure of the immediate phenotypic
41 quality of individuals within a population and can serve as a rough proxy for their
42 relative fitness - animals in 'good' condition can fulfil their own energetic needs
43 and store spare resources for future use, potentially deriving fitness benefits over
44 the long term (Speakman, 2001). Here, 'good condition' is taken to represent
45 some favourable range of body composition which may vary according to sex,
46 age or season; in practice, 'good condition' will be defined by some minimum
47 level or threshold below which growth and / or reproduction become
48 compromised.

49

50 Capital-breeding species acquire and store resources over a prolonged period
51 prior to breeding. Marine top predators such as true seals (*Phocidae*) accumulate
52 reserves by exploiting spatio-temporal aggregations of prey (Boyd, 2000;
53 Jönsson, 1997; Stephens, Boyd, McNamara, & Houston, 2009). Physiological
54 mechanisms for energy storage allow for resources to be 'banked' for use during
55 reproductive episodes when feeding does not occur. Within this 'capital-breeding'
56 life history pattern, intrinsic phenotypic and genotypic quality, age and experience
57 may contribute to individual variability in energy resources. Environmental
58 variation (either as prey availability or physical environmental conditions) can

59 impact body condition and, interacting with intrinsic variability, ultimately affect
60 population demographics (Ferguson et al., 2017; Tartu et al., 2017). It is of
61 fundamental interest to determine the drivers and consequences of intrinsic and
62 extrinsic variability between individuals.

63

64 Capital-breeding phocid seals have short lactation periods during which maternal
65 resources are rapidly and efficiently transferred to offspring. Some species enter
66 a total or partial fast during lactation, relying on endogenous energetic capital to
67 fulfil maintenance of metabolic and reproductive costs (Champagne, Crocker,
68 Fowler, & Houser, 2012; Crocker & Costa, 2009). Maternal mass at parturition
69 has emerged as a useful measure predicting lactation performance and
70 strategies, maternal expenditure and offspring size, and future breeding
71 likelihood in some phocid species (Bowen, Iverson, Boness, & Oftedal, 2001;
72 Boyd, 2000; Pomeroy, Fedak, Rothery, & Anderson, 1999; Wheatley, Bradshaw,
73 Davis, Harcourt, & Hindell, 2006). Total body mass is relatively straightforward to
74 measure but important aspects of lactation, pup mass and survival may be better
75 explained with reference to changes in water, lipid and protein body components
76 (Bennett, Speakman, Moss, Pomeroy, & Fedak, 2007; Crocker & Costa, 2009;
77 Mellish, Iverson, & Bowen, 1999; Reilly, Fedak, Thomas, Coward, & Anderson,
78 1996).

79

80 There is considerable debate over which physiological, morphometric or
81 biochemical metrics most accurately and appropriately capture body

82 composition, and how these may differ between taxa and seasons (Hayes &
83 Shonkwiler, 2001). Typically in field studies, detailed information on body
84 composition is not available and measures of external morphology are used to
85 calculate ratio-based or residual-based body condition indices (Hayes &
86 Shonkwiler, 2001). Gross body mass has also been used to explain reproductive
87 performance in grey seals (Bowen, Iverson, McMillan, & Boness, 2006; Boyd,
88 2000; Pomeroy et al., 1999). Direct measurement using isotopic methods during
89 the reproductive period allows body components to be quantified (Reilly et al.,
90 1996). Within the breeding episode, the balance of resources available in terms
91 of lipid and protein may govern how those reserves are allocated. Crocker,
92 Webb, Costa, and le Boeuf (1998) found protein use increased with declining
93 adiposity in fasting northern elephant seals and suggested that protein loss could
94 ultimately limit the extent of maternal investment. If energy reserves are depleted
95 too heavily and females leave the colony in relatively poor condition, this may
96 also impact on the success of their subsequent pregnancy (Boyd, 1984, 2000).
97 Pup size at weaning and on departure is positively related to early survival at sea
98 (Bennett et al., 2007; Bowen, den Heyer, McMillan, & Iverson, 2015; Hall,
99 McConnell, & Barker, 2001) and to subsequent recruitment into the breeding
100 population (Bowen et al., 2015) in grey seals. Pups' ability to withstand the post-
101 weaning fast and survive early months at sea may also depend on their mothers'
102 milk composition (Bennett et al., 2007). The composition of stored resources
103 available to the mother may therefore have important consequences for her pup.
104

105 Logistical difficulties in measuring standardized body composition in free-ranging
106 animals have meant that for many marine mammals, estimates of condition have
107 been obtained from commercial or subsistence hunts (e.g. Hammill & Sauv e,
108 2017; Harwood et al., 2015). While these studies allow direct and complete
109 sampling of the animals, they may suffer from sampling bias and, as cross-
110 sectional samples, cannot impute any longitudinal aspects for individual life
111 histories. In contrast, if non-lethal techniques can be used to obtain condition
112 estimates on animals which can be captured, released, and recaptured, repeated
113 measures can be made in different years (Bowen et al., 2015; Pomeroy et al.,
114 1999). Provided animal life history is not appreciably affected by the
115 measurement process, important additional information about the causes and
116 consequences of changes in individual condition may then be gained from these
117 longitudinal studies.

118

119 Grey seals (*Halichoerus grypus*) are capital-breeding phocids that reproduce on
120 the coastlines of the North Atlantic. Individually identified females have been
121 followed over multiple years at two breeding colonies in the UK, providing
122 information on individual variability in reproductive success (Pomeroy et al.,
123 1999) and body composition. The two study sites are located in regions
124 characterized by different oceanographic features and contrasting population
125 trajectories. North Rona (NR) is located off the UK's Atlantic coast (Figure 1).
126 Pup production has been in decline at this colony since the mid-1990s and there
127 is evidence that recruitment is low (Pomeroy, Smout, Moss, Twiss, & King,

128 2010). The Isle of May (IM) is located in the central North Sea Here, annual pup
129 production rose steadily between the 1970s and 1990s to stabilize at
130 approximately 2,000 as newer colonies nearby have been formed (SCOS, 2017).

131

132 Factors influencing variation in grey seal maternal postpartum body composition,
133 expressed as the ratio of lipid to protein mass, and the consequences for
134 mothers and pups were investigated, comparing individual body composition at
135 NR and IM. Specific objectives were: (1) characterizing inter-annual variation in
136 maternal postpartum body composition; (2) linking changes in individual maternal
137 body composition between breeding episodes; (3) exploring consequences of
138 maternal postpartum body composition for expenditure and for offspring size
139 within a breeding episode.

140

141 **2. METHODS**

142 **2.1 Field sampling**

143 All procedures involving animals in this study were performed under UK Home
144 Office project license 60/4009 or preceding versions and conformed to the UK
145 Animals (Scientific Procedures) Act, 1986. The research was approved by the
146 University of St Andrews Animal Welfare and Ethics Committee. Tritium use was
147 licensed under SEPA regulations.

148

149 Lactating grey seals were studied at two breeding colonies: North Rona (NR),
150 Scotland (59°06'N, 05°50'W) and the Isle of May (IM), Scotland (56°11'N,

151 02°33'W) (Figure 1). Individual females were identified by brand, flipper tags or
152 pelage patterns. Parturition and weaning dates for mothers were recorded from
153 detailed behaviour observations from hides. If not directly observed, the birth
154 date of the pup was estimated from indicators of age such as the presence of the
155 umbilicus and its size at first capture. The estimated birth date was the first day
156 of lactation. Weaning was established when the mother had left the pup. Pupping
157 was classed as successful if the pup survived to weaning and weighed more than
158 30 kg by the end of lactation (Pomeroy et al., 1999). All animals included in the
159 present analysis pupped successfully.

160

161 A subset of known females was captured for morphometric measurements and
162 determination of body composition by hydrogen isotope dilution. A total of 122
163 complete captures were available from 2003, 2004, 2007, 2008, 2009, 2010 &
164 2011 at NR and 133 complete captures from 2004, 2007, 2008, 2009, 2011,
165 2012 & 2013 at IM. Each female was captured once in early lactation and again
166 in late lactation. At each capture, females were anaesthetized with a mass
167 specific intramuscular dose of Zoletil 100™ and weighed to the nearest 0.2 kg.
168 Pups were weighed with a spring balance to the nearest 0.2 kg.

169

170 After immobilization of the mother, a 10 mL blood sample was recovered from
171 the extradural vein into heparinized vacutainers to measure background
172 hydrogen isotope activity. A weighed dose (to the nearest 0.1 mg) of tritiated
173 water (HTO) was injected into the extradural vein. The syringe was flushed with

174 blood three times to ensure the entire dose was administered. After an
175 equilibration period of 3 – 5 h, the female was recaptured to obtain a tritium-
176 enriched blood sample (10 mL). All blood samples were centrifuged within 6 h
177 after capture. Plasma was separated and stored at -20°C until analysis.

178

179 **2.2 Hydrogen isotope analysis**

180 Samples collected between 2007 and 2013 were prepared via the distillation
181 method (modified from Ortiz, Costa, & Le Boeuf, 1978; and Arnould, Boyd, &
182 Speakman, 1996). Plasma water was recovered from 200 µl aliquots of blood
183 plasma by direct distillation into pre-weighted plastic scintillation vials; 4 mL of
184 liquid scintillation cocktail (Ecoscint A, National Diagnostics, UK) was added to
185 plasma water after re-weighing vials, shaken for 5 s and then left overnight in a
186 dark refrigerator before analysis. All plasma samples were prepared in duplicate
187 and counted on a Packard 2000 Tri-Carb liquid scintillation counter for 10 min
188 with correction for quenching by external standards. Results were reported as
189 decays per min (DPM), and converted to specific activity (DPMg⁻¹) using the
190 mass of recovered plasma water.

191

192 Samples collected between 2003 and 2004 were analysed using whole plasma
193 as per the methods of Pomeroy et al. (1996). Approximately 300 µl of plasma
194 was pipetted into pre-weighed liquid scintillation vials in duplicate. The vial was
195 re-weighed before adding 10 mL of scintillation fluid (Ultima Gold, Perkin Elmer,
196 UK) and left overnight in a dark refrigerator prior to determination of specific

197 activity via liquid scintillation using the protocol described above. Plasma water
198 content was determined by weighing, drying, and re-weighing a 200 µl aliquot of
199 plasma in duplicate. Specific activity determined in the whole plasma sample was
200 then corrected for water content.

201

202 To test if the two methods of preparing samples introduced significant differences
203 in the estimation of specific activity, the following protocol was used. A sample of
204 plasma was obtained from a captive grey seal at the Sea Mammal Research
205 Unit. The sample was artificially enriched with a quantity of HTO injectate and
206 diluted to mimic the approximate *in vivo* dilution (1:20,000). The sample was split
207 and 25 subsamples were prepared for liquid scintillation analysis using each of
208 the two methods described above (n = 25 samples using each method). An
209 analysis of variance test was used to test for significant effect of preparation
210 method. There was no significant effect of preparation method on the specific
211 activity of an artificially enriched plasma sample ($F_{(1,48)} = 0.263$; $MSE = 48895$; p
212 $= 0.61$), suggesting that it was unlikely that differences in 2003 and 2004 results
213 compared to 2007:2013 results were due to the different methods of analysis.

214

215 Standards for the injectate from the year of the study were prepared by
216 gravimetric dilution of unused injectate to mimic approximate *in vivo* dilution. 200
217 µl of the diluted injectate was added to 4 mL of liquid scintillation fluid (EcoScint
218 A, National Diagnostics, UK) and counted in the same manner as plasma
219 samples.

220

221 **2.3 Maternal body composition calculations**

222 Body composition was estimated according to the methods of Reilly and Fedak
223 (1990). Dilution space, D , was calculated from the mean specific activity of the
224 seal plasma duplicates and injectate samples according to equation (1):

225

$$226 \quad (1) \quad D_{HTO} = \left(\frac{SA_{inj} HTO_{admin}}{SA_{eq} - SA_{ini}} \right) 0.001$$

227

228 where SA_{inj} is the specific activity of the injectate for the year of sampling,
229 HTO_{admin} is the dose of tritiated water administered to the seal and SA_{eq} and SA_{ini}
230 are the specific activity of equilibrium and initial (background) samples,
231 respectively. Reilly and Fedak (1990) determined an empirical relationship
232 between isotope dilution space and total body water (TBW) from four grey seals
233 (two mother-pup pairs) which was used to correct D_{HTO} to TBW.

234

$$235 \quad (2) \quad TBW = -0.234 + 0.971D_{HTO}$$

236

237 Evidence suggests that the rate of total body mass loss is relatively constant over
238 the lactation period (Fedak & Anderson, 1982). The daily rates of water and
239 mass loss (kg d^{-1}) were assumed to be constant and were calculated from the
240 change between early and late lactation captures. Median number of days
241 between captures was 11 days (range: 6 to 17). Maternal postpartum mass
242 (MPPM) and TBW were extrapolated by adding the product of the daily mass

243 loss and the number of days since parturition to mass at first capture. Similarly,
244 the product of the daily mass loss and the number of days between last capture
245 and weaning was subtracted from mass at last capture to extrapolate to maternal
246 wean mass (MWM) and TBW at weaning. Proportion body water, P_{water} ,
247 postpartum and at weaning was calculated using extrapolated masses.

248

249 Equations from Reilly and Fedak (1990) were used to predict proportion lipid
250 (Eqn 3) and protein (Eqn 4) using observed P_{water} values within the range of the
251 original Reilly and Fedak (1990) data ($P_{water} = [0.43, 0.68]$).

252

253 (3) $P_{lipid} (\%) = (105.1 - 1.47 \times P_{water}(\%)) \times MASS \text{ (kg)}$

254

255 (4) $P_{protein} (\%) = (0.42 \times P_{water}(\%) - 4.75) \times MASS \text{ (kg)}$

256

257 where P_{water} and $MASS$ refer to these measurements at parturition and at
258 weaning. Masses of lipid and protein components at the beginning and end of
259 lactation were calculated using estimated MPPM and MWM. To compare lipid
260 and protein together across individuals a metric of body composition that
261 reflected animal fatness relative to lean mass was calculated. Maternal
262 composition was expressed as the ratio of lipid mass to protein mass at the
263 beginning (maternal postpartum condition, MPPC) and at the end of lactation
264 (maternal weaning condition, MWC). Relative expenditure of lipid and protein
265 over the breeding episode was estimated as the difference between masses of

266 respective body components at postpartum and at weaning divided by their
267 postpartum mass. Acronyms of all body composition metrics and their meaning
268 are given in Table 1.

269

270 **2.4 Data analyses**

271 MPPC was determined for all mothers in the study. However, some covariates
272 were not always available for every study animal (e.g. weaning day, age).

273 Furthermore, while body composition observations for some mothers occurred in
274 several years most did not occur in consecutive years and observations from
275 other mothers occurred only once. Because information about all covariates for
276 every observation was not available to include in a single model, data subsets
277 were used which maximized the information available for each dependent /
278 covariate set of interest (see Table 2 for details of sample size used in each
279 analysis).

280

281 Temporal trends in all observations of MPPC at IM and NR were characterised
282 by fitting a generalized additive mixed model (model M1) to annual postpartum
283 body composition data using a Gaussian error distribution. Year was included as
284 a smooth term for each colony and individual was specified as a random effect.

285 Visual inspection was used to detect any significant temporal autocorrelation in
286 model residuals.

287

288 The effects of mother age and of immediate past reproductive history on MPPC
289 were tested (model M2). This was possible only for a subset of animals, where
290 data were available. Age was not included in M1 because there was an
291 imbalance in the number of animals that had been aged in each year between
292 NR and IM. At NR, the number of sampled known age mothers declined from $n =$
293 17 in 2003 to $n = 2$ in 2011. At IM, the number of known age mothers was
294 between 10 and 20 in each year. Therefore the effect of maternal age on MPPC
295 was considered separately in a linear mixed effects model, M2, along with
296 information on reproductive state in the previous breeding episode which was
297 available for all known age mothers. A quadratic term was included to allow for a
298 non-linear relationship between age and MPPC. The impact of reproductive state
299 in the previous year on MPPC was examined by including a breeding state
300 covariate ('pup') coded as 1 (individual was seen on the colony and weaned a
301 pup successfully in the previous year), or 0 (all other conditions). An interaction
302 between age and the categorical covariate of colony (IM, NR) allowed for
303 different age-related effects at each site. To account for potential annual effects
304 specific to each colony a random intercept term of year within colony was added.
305 An additional random intercept for each individual was included to estimate the
306 general nature of variation among individuals while allowing for repeated
307 measures on some individuals.

308

309 For a limited number of mothers, body composition samples were available in
310 consecutive breeding episodes providing an opportunity to assess longitudinal

311 changes in expenditure and body composition. The relationship between relative
312 expenditure in terms of lipid (LEXP) or protein (PEXP) and the difference in
313 postpartum lipid (Δ MPPL) or protein mass (Δ MPPP) between consecutive
314 breeding episodes (models M3 and M4) was examined to investigate if high
315 expenditure of lipid or protein in one year incurred a cost to the mother in the
316 following breeding episode in terms of reduced absolute postpartum lipid or
317 protein mass. The model was fitted with a generalised additive model after initial
318 data inspection suggested non-linear relationships. A fixed effect for colony (IM,
319 NR) was included to allow for any overall difference in expenditure between
320 colonies.

321

322 Having explored potential drivers of variation in postpartum body composition,
323 the consequences of that variation within a breeding episode was explored next.
324 Mothers in better condition may be more capable of expending a larger
325 proportion of lipid stores during a breeding episode and also be capable of
326 sparing protein by meeting the majority of energetic needs with lipid (Crocker et
327 al., 1998; Fedak & Anderson, 1982). The relationship between MPPC and the
328 relative expenditure of each body component (LEXP, PEXP) within a breeding
329 episode was characterized using a mixed effects model with a random effect for
330 individual and year nested within colony (models M5 and M6). A difference in
331 expenditure between colonies was tested for by including a fixed effect for colony
332 (IM, NR). MPPM was included in both models to account for any effect of
333 maternal size on MPPC.

334

335 Relative expenditure of lipid and protein contributes to variation in maternal body
336 composition at weaning (MWC). Mothers expending a higher proportion of their
337 resources, and those leaving the colony in poorer condition, might incur a cost to
338 reproductive output (attendance and pupping) the following year (Boyd, 2000;
339 Pomeroy et al., 1999). The association between MWC in one year and the
340 probability of producing a pup in the subsequent year was explored using a
341 mixed effects logistic model. Random effects were included to take account of
342 variation among individuals and years (model M7).

343

344 To explore how maternal state at parturition influenced one measure of pup
345 quality – pup weaning mass (PWM) – body composition, relative lipid
346 expenditure, postpartum mass and maternal age were included in a multiple
347 regression with PWM as the response variable (model M8). Average PWM was
348 allowed to vary in IM and NR by including a fixed effect for colony. Covariates
349 were included in a linear mixed effect model with a random effect for individual
350 and year nested within colony. A Gaussian error distribution was specified. Multi-
351 collinearity in the predictor variables was assessed by calculation of variance
352 inflation factors (Fox & Weisberg, 2011).

353

354 Annual colony average MPPC estimates from model M1 were related to
355 independent survey estimates of pup production at each colony (SCOS, 2016)

356 using a general linear model with Gaussian error distribution (M9) to determine if
357 average maternal condition was related to trends in local pup production.

358

359 The *lme4* package was used to fit linear mixed effects models (Bates, Mächler,
360 Bolker, & Walker, 2015) and the *mgcv* package (Wood, 2011) to fit generalised
361 additive mixed models in the R statistical package (R Core Team, 2018).

362 Determining the degrees of freedom and p-values in mixed effects models is not
363 straightforward (Bates et al., 2015). For those fitted with *lme4*, the significance of
364 terms within the model was evaluated by profiling of 95% confidence intervals
365 (CI) on parameter estimates. Where 95% CI encompassed zero, the term was
366 not considered significant at the 5% in explaining variation in observations.

367 Marginal ($R^2_{GLMM(m)}$; fixed effects only) and conditional ($R^2_{GLMM(c)}$; fixed and
368 random effects) deviance explained was assessed for each fitted model
369 (Nakagawa & Schielzeth, 2013) implemented in the *MuMIn* package in R
370 (Bartoń, 2016). All continuous variables were centred to aide in model
371 convergence and all statistical analyses were performed in the R statistical
372 programme (R Core Team, 2018).

373

374 **3. RESULTS**

375 Summary statistics of body measurements can be found in Table 2. Postpartum
376 mass was higher at NR than IM but average body compositions were not
377 significantly different (Table 2). A typical postpartum grey seal mother in our
378 dataset was ca. 27% lipid, 18% protein and 53% water with the remaining 2%

379 attributable to mineral components. Therefore an 'average seal' immediately after
380 parturition had ca. 1.5 times more lipid than protein (i.e. MPPC = 1.5). At
381 weaning, an average mother's body composition was ca. 15% lipid and 21%
382 protein, giving an MPPC ca. 0.75.

383

384 Non-linear trends in maternal MPPC were different between the colonies and
385 included lower values at IM in 2004 and higher values at NR in 2003 & 2004
386 (Figure 2; M1, Table 3). There was a contrast in the temporal trends in MPPC at
387 the two colonies: the year(s) with high MPPC at IM (2009, 2011) corresponded to
388 the lowest MPPC years at NR while the lowest MPPC year at IM (2004)
389 corresponded to one of the highest at NR.

390

391 A subset of mothers for which MPPC was estimated were of known age, and had
392 information on presence and pupping in the previous year ($n = 111$ observations
393 from 59 mothers at IM and $n = 53$ observations from 26 mothers at NR). When
394 reproductive state in the previous year and a non-linear effect of age were
395 included in a mixed effects model of MPPC, there was no significant effect of
396 either covariate and no evidence for a difference between IM and NR (M2, Table
397 3).

398

399 A total of 38 consecutive observations of individual MPPL and MPPP were
400 available from 29 mothers. There was a significant overall negative relationship
401 between PEXP and Δ MPPP. Mothers that expended a high proportion of their

402 postpartum protein mass (>25%) during a breeding episode returned the
403 following year with smaller postpartum protein stores, although some exceptions
404 were evident (Fig. 3). This relationship did not differ significantly between IM and
405 NR (Figure 3; M4, Table 3) although PEXP was, on average, greater at NR
406 (Table 2). In contrast, the change in lipid mass between consecutive breeding
407 episodes was not significantly related to lipid expenditure at either IM or NR,
408 suggesting little evidence for a tangible cost to subsequent body composition
409 from high expenditure of lipid, nor of a benefit from lipid sparing.

410

411 Mothers that had larger amounts of lipid relative to protein mass at postpartum
412 expended relatively more of their lipid within the breeding episode. A one-unit
413 increase in MPPC was associated with an increase in LEXP expenditure of
414 18.29% (95% CI [7.31, 27.80]) (Figure 4a; M5, Table 3). Protein use over the
415 lactation period was negatively associated with MPPC (Figure 4b; M6, Table 3).
416 A one-unit increase in MPPC resulted in a reduction in PEXP of 10.6% (95% CI [-
417 14.42, -6.46]). Thus, one consequence of low MPPC was a greater use of protein
418 over the breeding fast.

419

420 Despite the consequences of relative maternal body composition at postpartum
421 for overall expenditure (on pup and to meet maternal metabolic demands) within
422 the breeding episode, there was little evidence that mothers leaving the breeding
423 colony in poor condition (low MWC) were less likely to attend the colony in the
424 following breeding episode at either IM or NR (p-values all > 0.7; M7, Table 3).

425

426 Pup weaning mass was positively associated with maternal postpartum mass in
427 the two colonies but similarly-sized mothers produced heavier pups at NR than at
428 IM (Figure 5; M8, Table 3). On average, for every 10 kg increase in MPPM, PWM
429 increased by an average of 1.6 kg and pups at NR were 7.9 kg heavier. Maternal
430 postpartum condition, relative lipid expenditure and maternal age were not
431 significant predictors of PWM. Variance inflation factors were less than 2 for each
432 parameter included in the model.

433

434 Although based on a limited number of years, the annual fits of MPPC from M1
435 were significantly and positively related to pup production at NR but not IM (M9,
436 Table 3).

437

438 **4. DISCUSSION**

439

440 Empirical estimates of body composition of a capital-breeding pinniped were
441 obtained from an individual-based long-term study at two UK breeding colonies.
442 Temporal trends in maternal condition differed between two grey seal colonies
443 with contrasting trends in pup production, but the effect of intrinsic factors on
444 individual body composition or expenditure appeared to be similar. There was no
445 evidence of an age effect on maternal body composition. Despite a similar
446 relationship between maternal postpartum body composition and body

447 component expenditure at the colonies, average pup weaning masses at IM were
448 less than those achieved by similarly-sized mothers at NR.

449

450 **4.1 Individual variation in maternal body composition**

451 In this study grey seal MPPM ranged from 121 kg on IM to 258 kg on NR and
452 lipid mass at parturition ranged from 47 kg at IM to 70 kg at NR. Clearly the
453 absolute resources available to breeding females at these extremes are very
454 different and set proximate limits on potential pup weaning masses. Determining
455 the variation in mothers' stores of lipid and protein components in animals of
456 markedly different sizes was made accessible using the relative measures
457 MPPC, LEXP, PEXP.

458

459 No significant relationship was detected between age and measures of body
460 composition from the subset of known age females in the present analysis (M2),
461 even though a quadratic age term allowed for potential differences in body
462 condition between early years, prime breeding years and senescence. Evidence
463 of age-related changes in maternal body mass and composition from other
464 capital-breeding pinnipeds is equivocal. There was little evidence for an
465 association between maternal age and postpartum lipid content of 40 female
466 Weddell seals (Wheatley et al., 2006), and Pomeroy et al. (1999) found no
467 association between inter-annual changes in MPPM and age of female grey
468 seals at NR. In a long-term study tracking individual female grey seal
469 reproductive performance over several years, Bowen, Iverson, McMillan, and

470 Boness (2006) demonstrated declines in multiple measures of reproductive
471 performance in older mothers but noted the findings could not be explained as
472 the result of reduced maternal body condition. In view of the lack of significant
473 age-related effects on MPPC for the subset of aged mothers in the present
474 analysis, the inter-annual changes in MPPC seen in the larger dataset (M1) are
475 unlikely to be due simply to differences in the ages of mothers included in the
476 study.

477

478 The present showed a positive association between maternal postpartum mass
479 and pup wean mass, as did Pomeroy et al., (1999). However, neither MPPC,
480 LEXP, maternal age, nor pup sex were significant in a full model to explain PWM,
481 which also included MPPM (M8). This is perhaps unsurprising given that mass is
482 only one of several measures of pup quality. Mothers at NR produced heavier
483 pups at higher MPPM than did those at IM (Figure 5). NR mothers were on
484 average heavier than those at IM and it is likely that they gave birth to heavier
485 pups (Fedak & Anderson, 1982), accounting for some of the offset in pup
486 weaning mass. While pup size has been positively related to early survival at IM
487 (Hall et al., 2001), it would be interesting to know if this result were generalizable
488 across pups from different colonies or if a similar but separate relationship exists
489 for those, larger, animals on the Atlantic coast. Body composition of pups was
490 not available for this study but is likely to also be important in early development
491 and for survival (Bennett et al., 2007). In the present study, maternal postpartum
492 body composition did not appear to be a better indicator of pup quality (as

493 measured by mass) than maternal postpartum mass. Thus, at least within a
494 colony, maternal postpartum mass may be a sufficient proxy for predicting
495 potential pup size.

496

497 **4.2 Longitudinal effects – change and consequences**

498 Sequential observations of free-ranging seals body composition are rare in the
499 literature. In this study, pupping success in the previous year did not significantly
500 affect MPPC (M2). However, the present study assumed that females not seen
501 on the colony also did not pup in the non-observed breeding episode. While
502 breeding site fidelity has been high at these colonies (Pomeroy, Twiss, &
503 Redman, 2000), it is possible that females not observed on the colony pupped
504 successfully elsewhere.

505

506 Previously, grey seal mothers at NR showing large proportional mass
507 expenditures during lactation in one year were associated with a decrease in
508 MPPM the following year (Pomeroy et al., 1999). Those results were extended
509 here to show the different allocations of body components during lactation. In the
510 subset of mothers measured in successive years, those that lost a larger
511 proportion of their postpartum protein mass in one breeding episode had
512 relatively smaller postpartum protein stores in the following season (M4).
513 Changes in postpartum protein mass were less than those of lipid mass, in
514 keeping with the need to conserve protein to meet basal metabolic demands
515 (Champagne et al., 2012; Costa, 2009). Mothers may modulate resource

516 allocation to breeding based on their body composition state at the start of the
517 breeding season, which is affected by foraging success over the inter-breeding
518 period as well as the allocation of resources to reproductive expenditure in the
519 previous year.

520

521 Importantly, there were no significant differences in the relationships detailed
522 above between IM and NR suggesting that individual mothers at a growing (IM)
523 and declining (NR) colony used body resources similarly to produce pups. This
524 may signal that differences in the marine environment where these animals
525 forage, rather than differences in the intrinsic factors affecting maternal body
526 composition (such as age or past reproductive allocation of resources), could be
527 responsible for the colony-specific temporal patterns in maternal body
528 composition.

529

530 Results from the longitudinal aspect of the present study linked variation in
531 maternal expenditure in one breeding episode to maternal resources in the
532 following year. Within a breeding episode, MPPC was an important determinant
533 of maternal expenditure in terms of both lipid and protein mass (M5 & M6). The
534 present study found the amount of protein utilized over the breeding season was
535 negatively related to initial MPPC: mothers with more lipid relative to protein at
536 the start of the breeding episode season utilized less of their protein reserves
537 (relative to body mass) during lactation. This evidence of increased protein
538 conservation in animals with higher initial fat reserves is consistent with evidence

539 from several other pinniped species (see references in Champagne et al., 2012).
540 Such mothers were able to lose proportionately more of their mass in terms of
541 lipid. Maternal mass and resource transfer efficiency is high in this species
542 (Fedak & Anderson, 1982; Pomeroy et al., 1999; Reilly et al., 1996). This would
543 suggest that mothers with a high MPPC at the start of the lactation period are
544 able to expend more on their offspring, potentially weaning a fatter pup.

545

546 Females must balance the drive to maximize expenditure on their offspring with
547 the conflicting demands of their own metabolic maintenance both during
548 lactation, and after leaving the colony. Females leaving the colony with low lipid
549 reserves relative to protein mass may be less likely to return to the colony the
550 following season because poor condition has been related to delayed
551 implantation (Boyd, 1984). However, there was little evidence that MWC affected
552 the odds of an individual returning to either colony the following year from the
553 present data (M7). The same considerations about equating absence at the
554 colony with a failure to pup discussed above also pertain here. Non-returning
555 females may have gone elsewhere to breed, or skipped a breeding episode; the
556 physiological or behavioural factors involved in these two outcomes may be quite
557 different. Without the ability to track departing females through to the next
558 breeding season, it is not easy to make the potentially important distinction
559 between them.

560

561 **4.3 Colony level effects of body composition**

562 Mean maternal postpartum body composition at NR and the IM showed different
563 temporal trends although there was considerable intra- and inter-year variation at
564 both colonies (M1, Figure 2). The lack of temporal correspondence in trends of
565 average body conditions (Figure 2) suggests that there is no single common
566 environmental driver on maternal condition and that colony-level trends could be
567 related to local scale environmental variation altering prey availability and seal
568 foraging success in the inter-breeding interval. Adult female grey seals around
569 Britain are most likely to forage in the region containing their breeding colony
570 (Russell et al., 2013). The marine characteristics surrounding NR in the NE
571 Atlantic, and the IM, within the North Sea, are substantially different. As long-
572 lived and wide-ranging predators, seals should be buffered from short-term or
573 local fluctuations in foraging success. Nevertheless, long-term and broad-scale
574 consequences of environmental change have been documented in several
575 pinniped species. The long-term decline in number and body size of Steller sea
576 lions (*Eumetopias jubatus*) in the Gulf of Alaska is thought to be at least partially
577 due to nutritional stress due to reduced availability of high-quality prey and their
578 replacement by less nutritious species (Trites & Donnelly, 2003). Variation in
579 harp seal blubber thickness in the Barents Sea has been related to the
580 abundance of different prey groups (Øigård, Lindstrøm, Haug, Nilssen, & Smout,
581 2013). Ferguson et al. (2017) found long-term declines in ringed seal blubber
582 thickness related to changing marine conditions in the Hudson Bay (longer
583 periods of open water, ENSO index and NAO index). The authors of the latter
584 study noted concomitant changes in ringed seal diet composition and a general

585 decline in pup production in the region. Long-term monitoring of southern
586 elephant seals on Macquarie Island has demonstrated links between
587 environmental conditions and maternal condition and expenditure; smaller
588 mothers tended to invest relatively more in male pups during favourable years,
589 providing increased likelihood of their pups surviving the first year (McMahon,
590 Harcourt, Burton, Daniel, & Hindell, 2017). The present study found a decline in
591 maternal postpartum condition between 2003/2004 and subsequent years at NR
592 was associated with declining pup production, and which may also be linked to
593 changes in environmental conditions impacting foraging success, similar to that
594 described for southern elephant seals (e.g. Hindell et al., 2017).

595

596 Over the period of this study, grey seal pup production growth has slowed and
597 stabilized in the Hebrides while continuing to grow in the North Sea region
598 surrounding IM, particularly to the south (SCOS, 2017). Colony level
599 demographics at IM and NR reflect these changes: pup production at IM
600 increased by 17% from 1,953 in 2004 to 2,355 in 2012, and declined by 44%
601 from 970 in 2003 to 547 in 2012 at NR. Estimates of apparent survival and
602 fecundity are lower for females breeding at NR than at IM, and NR has lower
603 recruitment, consistent with the trend in pup production (Pomeroy et al., 2010,
604 Smout et al., 2011). Within observations from NR, the present study found a
605 positive relationship between average MPPC of monitored females and colony-
606 level pup production. Although average MPPC at NR declined, the mothers
607 included in the sample raised pups successfully in the years they were observed

608 at the colony. This decline in average condition of successfully breeding animals
609 may point more towards a decline in the number of animals managing to breed at
610 this colony, consistent with the hypothesis that environmental conditions for
611 these animals during foraging no longer produce sufficient resources to support
612 the historical breeding population, as suggested by lower fecundity estimates at
613 NR (Smout et al., 2011). The lack of association between average MPPC and
614 pup production at IM might be explained if in general, females breeding there
615 have access to and are successful in obtaining adequate food resources such
616 that their body composition, while showing some temporal variation overall, was
617 'sufficiently good' over the period of the study. Continued recruitment of new
618 breeders, consistent survival rates and adequate fecundity of breeding females
619 could then support continued growth of the IM colony and its neighbours.

620

621 Where seal populations are monitored to determine population status and trends,
622 destructive sampling (often from commercial hunts) offers cross-sectional
623 information, not just for demographic parameters such as age-specific survival
624 and fecundity but also for condition measures, including morphometrics such as
625 mass, length, girth and typically, blubber thickness or sculp mass. While blubber
626 thickness may be an index of seal condition, this gross measure ignores non-
627 blubber fat and must be taken from seals of the same age/reproductive state to
628 be informative. Non-destructive sampling such as that described here is more
629 labour intensive, and long term longitudinal studies require sustained support.
630 They have enabled a more complete assessment of the factors involved in

631 determining the variation and outcomes of MPPC at individual and colony levels,
632 revealing the effects of individual aging and sequential reproductive effort
633 (Bowen et al., 2006; Pomeroy et al., 1999). Some inter-individual variation in
634 MPPC may be due to past condition, but annual patterns in condition metrics at
635 the colony level may be indicators of environmental changes affecting foraging
636 success and the carrying capacity of the environment for the local seal
637 population.

638

639 NR mothers weaned large pups whose survival would be expected to be high,
640 but there has been little or no recruitment at NR (Pomeroy et al., 2010).

641 Therefore post-weaning factors (survival or emigration) must influence
642 recruitment to the natal breeding colony as much or more than PWM alone.

643

644 This study highlights the benefit of long-term, longitudinal monitoring at multiple
645 sites to contextualise patterns in conservation data. Detailed investigation of
646 individual quality, resource allocation and offspring production allows for the
647 mechanisms of observed changes in population dynamics to be better
648 understood. This demonstrates the difficulty of producing simple indicators of
649 population status or individual quality: without context, in the broadest ecological
650 sense, they will be of limited value.

651

652 **ACKNOWLEDGEMENTS**

653 The authors are grateful to the many colleagues past and present who assisted
654 with fieldwork, particularly S. Twiss. The long-term studies included in this paper
655 were funded by the Natural Environment Research Council through the grant
656 “SMRU Long-term measurement of marine mammal population structure,
657 dynamics and trophic interactions”, grant reference SMRU1001. PP was in
658 receipt of NERC grant no. NE/G008930/1 and Esmée Fairbairn Foundation
659 funding during the work. SCS was supported as a postdoctoral fellow in an
660 EPSRC award to RK and PP. The funding sources had no role in the planning,
661 execution, analysis or writing of this study.

662

663 **ORCHID**

664 Nora Hanson <https://orcid.org/0000-0002-0017-8963>

665

666 **REFERENCES**

- 667 Bartoń, K. (2016). *MuMIn: Multi-Model Inference*. Retrieved from [https://CRAN.R-](https://CRAN.R-project.org/package=MuMIn)
668 [project.org/package=MuMIn](https://CRAN.R-project.org/package=MuMIn)
- 669 Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting Linear Mixed-
670 Effects Models Using lme4. *Journal of Statistical Software*, 67, 1–48.
- 671 Bennett, K. A., Speakman, J. R., Moss, S. E. W., Pomeroy, P., & Fedak, M. A.
672 (2007). Effects of mass and body composition on fasting fuel utilisation in
673 grey seal pups (*Halichoerus grypus* Fabricius): an experimental study
674 using supplementary feeding. *Journal of Experimental Biology*, 210, 3043–
675 3053.

676 Bowen, W. D., Iverson, S. J., Boness, D. J., & Oftedal, O. T. (2001). Foraging
677 effort, food intake and lactation performance depend on maternal mass in
678 a small phocid seal. *Functional Ecology*, 15, 325–334.

679 Bowen, W. D., Iverson, S. J., McMillan, J. I., & Boness, D. J. (2006).
680 Reproductive performance in grey seals: age-related improvement and
681 senescence in a capital breeder. *The Journal of Animal Ecology*, 75,
682 1340–1351.

683 Bowen, William. D., den Heyer, C. E., McMillan, J. I., & Iverson, S. J. (2015).
684 Offspring size at weaning affects survival to recruitment and reproductive
685 performance of primiparous gray seals. *Ecology and Evolution*, 5, 1412–
686 1424.

687 Boyd, I. L. (1984). The relationship between body condition and the timing of
688 implantation in pregnant Grey seals (*Halichoerus grypus*). *Journal of*
689 *Zoology*, 203, 113–123.

690 Boyd, I. L. (2000). State-dependent fertility in pinnipeds: contrasting capital and
691 income breeders. *Functional Ecology*, 14, 623–630.

692 Champagne, C. D., Crocker, D. E., Fowler, M. A., & Houser, D. S. (2012).
693 Fasting Physiology of the Pinnipeds: The Challenges of Fasting While
694 Maintaining High Energy Expenditure and Nutrient Delivery for Lactation.
695 In McCue, M. D. (Ed.), *Comparative Physiology of Fasting, Starvation, and*
696 *Food Limitation* (pp. 309–336). Berlin, Heidelberg: Springer

697 Costa, D. P. (2009). Energetics. In Perrin, W. F., Würsig, B., & Thewissen, J. G.
698 M. (Eds.), *Encyclopedia of Marine Mammals (Second Edition)* (pp. 383–
699 391). London: Academic Press.

700 Crocker, D. E., & Costa, D. P. (2009). Pinniped Physiology. In Perrin, W. F.,
701 Würsig, B., & Thewissen, J. G. M. (Eds.), *Encyclopedia of Marine*
702 *Mammals (Second Edition)* (pp. 383–391). London: Academic Press.

703 Crocker, D. E., Webb, P. M., Costa, D. P., & Le Boeuf, B. J. (1998). Protein
704 Catabolism and Renal Function in Lactating Northern Elephant Seals.
705 *Physiological Zoology*, 71, 485–491.

706 Fedak, M. A., & Anderson, S. S. (1982). The energetics of lactation: accurate
707 measurements from a large wild mammal, the grey seal (*Halichoerus*
708 *grypus*). *Journal of Zoology*, 198, 473–479.

709 Ferguson, S. H., Young, B. G., Yurkowski, D. J., Anderson, R., Willing, C., &
710 Nielsen, O. (2017). Demographic, ecological, and physiological responses
711 of ringed seals to an abrupt decline in sea ice availability. *PeerJ*, 5.

712 Festa-Bianchet, M., Gaillard, J., & Jorgenson, J. T. (1998). Mass- and density-
713 dependent reproductive success and reproductive costs in a capital
714 breeder. *The American Naturalist*, 152, 367–379.

715 Fox, J., & Weisberg, S. (2011). *An R Companion to Applied Regression*
716 (Second). Thousand Oaks CA: Sage.

717 Hall, A. J., McConnell, B. J. M., & Barker, R. J. (2001). Factors affecting first-year
718 survival in grey seals and their implications for life history strategy. *Journal*
719 *of Applied Ecology*, 70, 138–149.

720 Hammill, M. O., & Sauvé, C. (2017). Growth and condition in harp seals:
721 evidence of density-dependent and density-independent influences. *ICES*
722 *Journal of Marine Science*, 74, 1395–1407.

723 Harwood, L. A., Smith, T. G., George, J. C., Sandstrom, S. J., Walkusz, W., &
724 Divoky, G. J. (2015). Change in the Beaufort Sea ecosystem: Diverging
725 trends in body condition and/or production in five marine vertebrate
726 species. *Progress in Oceanography*, 136, 263–273.

727 Hayes, J. P., & Shonkwiler, J. S. (2001). Morphometric indicators of body
728 condition: worthwhile or wishful thinking? In Speakman, J. R. *Body*
729 *Composition Analysis of Animals. A Handbook of Non-Destructive*
730 *Methods* (pp. 8–38). New York: Cambridge University Press.

731 Hindell, M. A., Sumner, M., Bestley, S., Wotherspoon, S., Harcourt, R. G., Lea,
732 M.-A., McMahon, C. R. (2017). Decadal changes in habitat characteristics
733 influence population trajectories of southern elephant seals. *Global*
734 *Change Biology*, 23, 5136–5150.

735 Jönsson, K. I. (1997). Capital and income breeding as alternative tactics of
736 resource use in reproduction. *Oikos*, 78, 57–66.

737 McMahon, C. R., Harcourt, R. G., Burton, H. R., Daniel, O., & Hindell, M. A.
738 (2017). Seal mothers expend more on offspring under favourable
739 conditions and less when resources are limited. *Journal of Animal*
740 *Ecology*, 86, 359–370.

741 Mellish, J. E., Iverson, S. J., & Bowen, W. D. (1999). Variation in milk production
742 and lactation performance in grey seals and consequences for pup growth

743 and weaning characteristics. *Physiological and Biochemical Zoology*, 72,
744 677–690.

745 Nakagawa, S., & Schielzeth, H. (2013). A general and simple method for
746 obtaining R² from generalized linear mixed-effects models. *Methods in*
747 *Ecology and Evolution*, 4, 133–142.

748 Øigård, T., Lindstrøm, U., Haug, T., Nilssen, K., & Smout, S. (2013). Functional
749 relationship between harp seal body condition and available prey in the
750 Barents Sea. *Marine Ecology Progress Series*, 484, 287–301.

751 Pomeroy, P. P., Fedak, M. A., Rothery, P., & Anderson, S. (1999).
752 Consequences of maternal size for reproductive expenditure and pupping
753 success of grey seals at North Rona, Scotland. *Journal of Animal Ecology*,
754 68, 235–253.

755 Pomeroy, P. P., Green, N., Hall, A. J., Walton, M., Jones, K., & Harwood, J.
756 (1996). Congener-specific exposure of grey seal (*Halichoerus grypus*)
757 pups to chlorinated biphenyls during lactation. *Canadian Journal of*
758 *Fisheries and Aquatic Sciences*, 53, 1526–1534.

759 Pomeroy, P. P., Twiss, S. D., & Redman, P. (2000). Philopatry, site fidelity and
760 local kin associations within grey seal breeding colonies. *Ethology*, 106,
761 899–919.

762 Pomeroy, P., Smout, S., Moss, S., Twiss, S., & King, R. (2010). Low and delayed
763 recruitment at two grey seal breeding colonies in the UK. *Journal of*
764 *Northwest Atlantic Fishery Science*, 42, 125–133.

765 R Core Team. (2018). *R: A language and environment for statistical computing*.
766 Vienna, Austria: R Foundation for Statistical Computing. Retrieved from
767 <https://www.R-project.org/>

768 Reilly, J. J., Fedak, M. A., Thomas, D. H., Coward, W. a. A., & Anderson, S. S.
769 (1996). Water balance and the energetics of lactation in grey seals
770 (*Halichoerus grypus*) as studied by isotopically labelled water methods.
771 *Journal of Zoology*, 238, 157–165.

772 Reilly, John J., & Fedak, M. A. (1990). Measurement of the body composition of
773 living gray seals by hydrogen isotope dilution. *Journal of Applied*
774 *Physiology*, 69, 885–891.

775 Ronget, V., Gaillard, J.-M., Coulson, T., Garratt, M., Gueyffier, F., Lega, J.-C., &
776 Lemaître, J.-F. (2018). Causes and consequences of variation in offspring
777 body mass: meta-analyses in birds and mammals. *Biological Reviews*, 93,
778 1-27.

779 Russell, D. J. F., McConnell, B., Thompson, D., Duck, C., Morris, C., Harwood,
780 J., & Matthiopoulos, J. (2013). Uncovering the links between foraging and
781 breeding regions in a highly mobile mammal. *Journal of Applied Ecology*,
782 50, 499–509.

783 Schick, R. S., New, L. F., Thomas, L., Costa, D. P., Hindell, M. A., McMahon, C.
784 R., ... Clark, J. S. (2013). Estimating resource acquisition and at-sea body
785 condition of a marine predator. *The Journal of Animal Ecology*, 82, 1300–
786 1315.

787 SCOS. (2016). *Scientific advice on matters related to the management of seal*
788 *populations: 2016* (SCOS Main Advice). Sea Mammal Research Unit.

789 SCOS. (2017). *Scientific advice on matters related to the management of seal*
790 *populations: 2017* (SCOS Main Advice). Sea Mammal Research Unit.

791 Sheldon, B. C., & West, S. A. (2004). Maternal dominance, maternal condition,
792 and offspring sex ratio in ungulate mammals. *The American Naturalist*,
793 163, 40–54.

794 Speakman, J. R. (Ed.). (2001). *Body composition analysis of animals: a*
795 *handbook of non-destructive methods*. Cambridge, UK ; New York:
796 Cambridge University Press.

797 Stephens, P. A., Boyd, I. L., McNamara, J. M., & Houston, A. I. (2009). Capital
798 breeding and income breeding: their meaning, measurement, and worth.
799 *Ecology*, 90, 2057–2067.

800 Tartu, S., Bourgeon, S., Aars, J., Andersen, M., Polder, A., Thiemann, G. W., ...
801 Routti, H. (2017). Sea ice-associated decline in body condition leads to
802 increased concentrations of lipophilic pollutants in polar bears (*Ursus*
803 *maritimus*) from Svalbard, Norway. *Science of the total environment*, 576,
804 409–419.

805 Trites, A. W., & Donnelly, C. P. (2003). The decline of Steller sea lions
806 *Eumetopias jubatus* in Alaska: a review of the nutritional stress
807 hypothesis. *Mammal Review*, 33, 3–28.

808 Wheatley, K. E., Bradshaw, C. J. A., Davis, L. S., Harcourt, R. G., & Hindell, M.
809 A. (2006). Influence of maternal mass and condition on energy transfer in

810 Weddell seals. *Journal of Animal Ecology*, 75, 724–733.
811 <https://doi.org/10.1111/j.1365-2656.2006.01093.x>
812 Wood, S. (2011). *mgcv: GAMs with GCV/AIC/REML smoothness estimation and*
813 *GAMMs by PQL*. Retrieved from [http://cran.r-](http://cran.r-project.org/web/packages/mgcv/index.html)
814 [project.org/web/packages/mgcv/index.html](http://cran.r-project.org/web/packages/mgcv/index.html)
815
816

817 **Table 1:** Definition of grey seal (*Halichoerus grypus*) body composition acronyms
818 used in the text and data analysis.

819

Abbreviation	Meaning
MPPM	Maternal postpartum mass (kg)
MWM	Maternal weaning mass (kg)
MPPL	Maternal postpartum lipid mass (kg)
MPPP	Maternal postpartum protein mass (kg)
MPPC	Maternal postpartum condition (MPPL/MPPP)
MWC	Maternal weaning condition (mass lipid at weaning/mass protein at weaning)
LEXP	Lipid expenditure (% MPPL)
PEXP	Protein expenditure (% MPPP)
PWM	Pup weaning mass (kg)

820

821

822

823 **Table 2:** Summary statistics of female grey seal morphometric and body
 824 composition data.
 825

Metric	Isle of May	n	North Rona	n
	(mean [95% CI])		(mean [95% CI])	
Postpartum mass (MPPM, kg)	179 [175, 183]	134	190 [187, 194]	122
Age¹	18 [8, 32]	116	18 [10, 32]	58
Postpartum lipid (%)	26.5 [25.6, 27.4]	134	26.9 [26.0, 27.8]	122
Postpartum protein (%)	17.7 [17.5, 18.0]	134	17.6 [17.3, 17.9]	122
Weaning lipid (%)	14.9 [13.5, 16.2]	94	15.3 [13.7, 17.0]	93
Weaning protein (%)	21.0 [20.6, 21.4]	94	20.9 [20.4, 21.3]	93
Postpartum condition (MPPC)	1.53 [1.46, 1.61]	134	1.56 [1.49, 1.64]	122
Weaning condition (MWC)	0.74 [0.66, 0.82]	94	0.79 [0.68, 0.89]	93
Lipid expenditure (LEXP, % MPPL)	60.8 [56.8, 64.9]	94	61.6 [57.3, 66.0]	93
Protein expenditure (PEXP, % MPPP)	20.3 [18.7, 21.9]	94	23.3 [21.2, 25.3]	93
Pup wean mass (kg)	43.7 [42.4, 45.1]	86	52.5 [50.9, 54.0]	92

826 ¹ Age given is median [minimum, maximum]

827

Table 3: Details of fitted models, method used, and results. Regression parameters are mean [95% confidence intervals]. Year of observation is indicated by the subscript i . Variance explained by fitted model is given by R^2 value. For linear mixed effects models, marginal R^2_m indicates variance explained by fixed effects alone and conditional R^2_c is an estimate of variance explained including random effects (Nakagawa & Schielzeth, 2013). In the model specifications, ‘s()’ indicates a smooth function; ‘x’ indicates an interaction term and ‘/’ indicates nesting.

Response	Fixed covariates	Random effects	n	Significant term(s)	p-value	β	R^2_m	R^2_c
M1 MPPC	s(Year) : Colony	Individual (n = 138)	255	s(year):IM s(year):NR	0.019 < 0.001		40	
M2 MPPC	(Age + Age ²) x Colony + Pup _[i+1]	Individual (n = 85), Year/Colony (n = 16)	164				6.6	42
M3 Δ MPPL(%)	s(LEXP _[i-1]) + Colony		38				22	
M4 Δ MPPP (%)	s(PEXP _[i-1]) + Colony		38	s(PEXP _[i-1])	0.012		15	
M5 LEXP	MPPC x Colony + MPPM x Colony	Individual (n = 111), Year/Colony (n = 15)	187	MPPC		18.29 [7.32, 27.80]	11	30
M6 PEXP	MPPC x Colony	Individual (n = 111), Year/Colony (n = 15)	187	MPPC		-10.62 [-14.42, -6.46]	28	49

M7	Pup _[t+1]	MWC x Colony	Individual (n = 107), Year/Colony (n = 15)	177			< 1	< 1
M8	PWM	MPPC x Colony + MPPM x Colony + LEXP x colony + Maternal age	Individual (n = 69), Year/Colony (n = 15)	117	Colony MPPM	7.86 [3.80, 12.12] 0.16 [0.11, 0.22]	47	74
M9	MPPC (M1) at IM	Pup production at IM		8				
	MPPC (M1) at NR	Pup production at NR		8	Pup production at NR	384 [118, 797]	19	

Figure 1: Map of the United Kingdom showing the location of the two grey seal breeding colony study sites, Isle of May (IM) in the North Sea and North Rona (NR) in the Atlantic.

Figure 2: Generalised additive mixed model (GAMM) smoothed temporal patterns in mean postpartum condition (MPPC, defined as the ratio of lipid to protein mass) of breeding female grey seals at Isle of May (IM) and North Rona (NR) colonies (line and 95% confidence intervals in grey). Circles represent observed values; filled circles indicate samples from known age mothers.

Figure 3: The relationship between change in postpartum protein mass in consecutive breeding episodes ΔMPPP and the proportion of protein expended PEXP in the first of those years.

Figure 4: Relationship between the proportion of lipid mass loss (LEXP) and maternal postpartum condition (MPPC) (a); and the proportion of protein mass loss (PEXP) and maternal postpartum condition (MPPC) (b).

Figure 5: Grey seal pup weaning mass (PWM, kg) increased with maternal postpartum mass (MPPM) at both the Isle of May (IM, solid line and filled triangles) and North Rona (NR, dashed line and open circles) breeding sites.