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Post-lactation mass recovery and metabolic hormone dynamics in adult female Weddell seals

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Abstract

Weddell seal (*Leptonychotes weddellii*) females lose substantial body mass across an intensive, nutritionally restricted lactation period and then must rapidly recover mass during the short Antarctic summer. In this study, we examined endocrine dynamics associated with mass loss across lactation and subsequent realimentation in Weddell seals, comparing patterns between seals that recently gave birth and demographically similar non-reproductive females (skip females) in McMurdo Sound, Antarctica. Postpartum seals near weaning (~35 days postpartum, n = 64) and skip females (n = 32) were handled during early austral summer (November/December) and rehandled in late summer (January/February). Body mass, body composition (% lipid), and a suite of metabolic hormones (growth hormone (GH), insulin-like growth factor (IGF)-I, cortisol, total thyroxine (tT_4), free thyroxine (fT_4), and total triiodothyronine (tT_3) and IGF binding protein (IGFBP)-2 and −3) were measured. Postpartum seals gained mass after weaning (0.98 ± 0.56 $kg{\cdot}day^{-1}$ (mean ± SD)), primarily as lean tissue rather than lipid, while their serum concentrations of tT_4 and fT_4, IGF-I, and cortisol increased. Their circulating GH and IGFBP-2 concentrations decreased and correlated negatively with mass. Skip females had greater body masses and lipid stores than postpartum seals at the end of the lactation period in early summer, but they lost mass (−1.03 ± 0.35 $kg{\cdot}day^{-1}$) and lipid stores over summer while their serum cortisol concentrations

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CRediT authorship contribution statement

Amy L. Kirkham: Writing – original draft, Visualization, Validation, Investigation, Data curation, Formal analysis, Conceptualization, Funding acquisition. **Julie P. Avery:** Writing – review & editing, Resources, Investigation. **Roxanne S. Beltran:** Writing – review & editing, Investigation, Data curation. **Jennifer M. Burns:** Writing – review & editing, Supervision, Resources, Project administration, Funding acquisition, Conceptualization.

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ygcen.2025.114706.

increased. Overall, body mass and composition of postpartum and skip females converged across summer. This convergence, likely driven in large part by contrasting endocrine profiles between the groups, may allow female Weddell seals to reach an advantageous seasonal body mass “set point” by onset of winter.

Keywords

Pinniped; Lactation; Metabolism; Body mass; Somatotropic axis; Thyroid hormones; Cortisol

1. Introduction

A fundamental challenge through the life histories of wildlife is reconciling imbalances in energy supply and demand (McNab, 2002). Food availability shifts with seasonal conditions and behavioral constraints, and life history events such as migration, hibernation, and rearing young can require large body stores of protein and lipid gained in advance to fuel these processes. Building these stores, expending them efficiently to meet needs that enhance fitness, and subsequently recovering stores is regulated in large part by metabolic hormones. Typical patterns in how these hormones relate to body mass changes in different species and scenarios are discussed further below.

Pinnipeds, which include true seals (phocids), eared seals (i.e., fur seals and sea lions; otariids), and walruses (*Odobenus rosmarus* spp.), have been the subject of numerous studies on the physiology of body mass changes because they often undergo large fluctuations in endogenous stores of protein and lipid associated with natural fasting periods (e.g., Crocker et al., 2012; Kelso et al., 2012; Khudyakov et al., 2019; Wheatley et al., 2006). For example, seal pups of some species fast after they are weaned before they are capable of capturing prey (Crocker and McDonald, 2022; Champagne et al., 2012), and adult male pinnipeds may fast and lose substantial mass while maintaining territories or harems during the breeding season (Costa and Maresh, 2022; Deutsch et al., 1990). A number of female phocids fast or reduce their food intake while they are nursing pups, meaning they take in little or no energy at the same time they are taxed with producing extremely rich milk (31 % to 65 % lipid and 5 to 14 % protein) (Champagne et al., 2012; Schulz and Bowen, 2004). Seal pups need such large quantities of lipid and protein, respectively, so they can build a blubber layer that allows them to thermoregulate in the marine environment and to fuel growth and development, including of musculature and oxygen stores that allow for effective underwater foraging (Burns et al., 2005; Castellini, 2009). After pups wean, adult female phocids similarly need to accumulate lipid and protein that was lost during lactation so they can effectively thermoregulate and forage (Rosen et al., 2007; Watts et al., 1993). Additionally, the annual molt typically occurs soon after weaning in adult females, so recuperating body stores is important to meet the energetic and protein costs of replacing pelage; these include the cost of reduced foraging while seals spend more time out of the water to keep skin warm (Beltran et al., 2018; Paterson et al., 2012; Worthy et al., 1992).

Adult female Antarctic Weddell seals (*Leptonychotes weddellii*) undergo some of the largest changes in body mass observed in pinniped annual cycles. Across a five to seven week

lactation period, nursing female Weddell seals reduce their foraging and lose more than a third of their body mass at rates between 2 and 6 $kg \cdot day^{-1}$ (averaging 1 % of body mass per day) as their pups triple in mass, growing from < 30 kg to > 90 kg (Reijnders et al., 1990; Wheatley et al., 2006). Energy mobilization for lactation leads to an average 56 % decline in total lipid stores and 29 % decline in total protein stores between birth and weaning (Wheatley et al., 2006). Weddell seals breed in late lactation and complete an annual molt in the months following weaning, meaning the major annual life history events of parturition, lactation, mating, and molt all occur during the limited window of austral summer (i.e., polar day) in Weddell seals' high-latitude environment (Fig. 1).

While body mass dynamics across lactation in Weddell seals have been described (Wheatley et al., 2006; Wheatley et al. 2008), previous studies have not addressed how postpartum Weddell seals recover lipid and protein stores following weaning and what endocrine patterns facilitate these mass gains. Recovery of body stores over summer is likely critical for Weddell seals to support molt, to increase chances of successful pregnancy, and to capitalize on the brief summer pulse in prey abundance and accessibility in an extreme polar environment (Beltran et al., 2021; Guinet et al., 1998; Lunn and Boyd, 1993; Wade and Schneider, 1992; Worthy et al., 1992). Endocrine dynamics associated with mass recovery in postpartum Weddell seals therefore may reflect an optimized pattern for efficient accrual of protein or lipid stores.

Metabolic hormones that impact body mass in mammals and likely play a role in postpartum Weddell seal mass recovery include cortisol, growth hormone (GH), insulin-like growth factor-1 (IGF-I), IGF-I binding proteins (IGFBPs), and free and total thyroxine (T_4) and triiodothyronine (T_3). Cortisol is commonly elevated in mammals in poor body condition or with limited food intake, where it generally has catabolic effects and triggers increased appetite or foraging (Arlt and Stewart, 2005; Bergendahl et al., 1996; Guinet et al., 2004). Circulating GH concentrations also increase during insufficient energy intake, helping to limit protein catabolism while promoting lipolysis and suppressing lipogenesis (Kersten, 2001; Møller et al., 2003). In well-fed animals, such as during realimentation, greater serum GH facilitates lean mass accretion in part by stimulating production of IGF-I via hepatic GH receptor signaling (Keogh et al., 2015a; Nordstrom et al., 2011; Velloso, 2008). Greater circulating IGF-I concentrations promote protein anabolism through multiple molecular pathways (Laron, 2001; Yoshida and Delafontaine, 2020). However, bioavailability, half-life, and tissue-specific utilization of IGF-I is regulated by IGFBPs (Bach, 2018; Breier, 1999). Of the six known IGFBP, IGFBP-2 and IGFBP-3 are sensitive to nutrient intake and nutritional status, are well studied in domestic animal lactation, and may impact nutrient utilization in a tissue-specific manner directly or indirectly via IGF-I (Allard and Duan, 2018; Clemmons, 2018). In general, elevations in circulating IGFBP-2 decrease IGF-I bioavailability during negative energy balance while elevations in circulating IGFBP-3 increase IGF-I bioavailability during periods of high food intake (Bach, 2018; Breier, 1999). T_4 and the more bioactive T_3 also strongly influence basal metabolic rate, thermogenesis, and somatic growth via numerous signaling pathways, generally increasing energetic expenditure (Brent, 2012; Yen, 2001). Correspondingly, mammals that need to conserve energy due to limited food intake or depleted body stores often have lower free or

total T_4 or T_3 levels (Atkinson et al., 2015; Bishop et al., 2009; Danforth and Burger, 1984; Verrier et al., 2012).

In this study, we aimed to characterize how the suite of metabolic hormones described above relate to postpartum recovery of protein and lipid stores in Weddell seals across the austral summer. We predicted that postpartum females would gain body mass quickly over summer and that their hormone concentrations would contrast with those of adult female seals that did not give birth in the current year (skip females), reflecting nutritional stress during the breeding period, i.e., late lactation. Additionally, we predicted that endocrine profiles of postpartum seals in late summer would reflect highly positive energy balance (e.g., elevated serum concentrations of IGF-I, IGFBP-3, total T_4 (tT_4), fT_4, and total T_3 (tT_3), and reduced concentrations of cortisol and IGFBP-2). We met study objectives by measuring serum hormone concentrations, body mass, and body composition in both postpartum Weddell seals and in skip females. Most individual seals were handled twice, and skip females provided points of contrast for patterns in postpartum females and important context for interpreting relationships between body store changes and hormones. Findings from this study show how endocrine physiology facilitates rapid mass recovery in free-ranging Weddell seals, a species that undergoes extreme body mass changes while living year-round at higher latitudes than any other mammal and facing steep seasonal constraints.

2. Methods

2.1. Study animals

To determine the patterns and drivers of post-weaning body store repletion in a polar pinniped, we studied adult female Weddell seals in McMurdo Sound, Antarctica in austral summers from 2013 to 2017. Study animals were of known age between 10 and 20 years old (fully grown/no longer increasing in length (McLaren, 1993)), as all were tagged as pups within a week of their birth, and all had given birth to at least two pups in their lifetimes (demographic data is available from an ongoing long-term population study (e.g., Garrott et al., 2012; Rotella et al., 2009)). In early austral summer (November and December), two groups of female seals were identified: (1) those that had given birth in the current year (postpartum females, n = 64) and (2) individuals that did not give birth in the current year, skipping one pupping season (skip females, n = 32). For postpartum females, first sampling occurred at approximately 35 days postpartum (DPP) in late lactation (Fig. 1). To facilitate recapture in late summer (January and February), a VHF tag (Sirtrack, Havelock North, NZ, 22 g) was attached to the hind flipper (Frankfurter et al., 2019). Of the original early summer cohort, 44 postpartum and 23 skip females were successfully resampled in late summer (Fig. 1). When individuals could not be relocated, Weddell seals of similar ages and reproductive histories were sampled to provide additional cross-sectional data (n = 13 postpartum females; n = 8 skip females).

2.2. Field Methods

Seals were captured with a hoop net and sedated with an intramuscular (IM) injection of ketamine and midazolam (2.0 and 0.1 $mg \cdot kg^{-1}$) (Mellish et al., 2010). Ten minutes after the initial injection, an intravenous (IV) line was established in the extradural vein, and the seal

was maintained at the appropriate plane of anesthesia throughout all procedures (~2 h) with IV injections of ketamine and/or midazolam as needed. Seals were weighed (±1.0 kg) using a sling, tripod, and hanging scale (MSI-7300 Dyna-Link 2, Rice Lake Weighing Systems, Rice Lake, WI). Standard length (straight length from the tip of the nose to the tip of the tail) was measured (±1.0 cm). Body composition percentage metrics (percent lipid and percent protein) were estimated from total body water calculations using the isotope dilution method with tritiated water and total body mass values following protocols detailed in Shero et al. (2014), with equations from Reilly and Fedak (1990). Total lipid mass and total protein mass values were calculated by multiplying body composition percentages by measured body mass, and total lean mass was calculated as body mass minus total lipid mass.

Blood samples for body composition and hormone analyses were collected in vacutainer tubes from the extradural vein. As soon as the IV line was established, prior to weighing, blood was collected in vacutainer tubes for analysis of serum hormone concentrations and other physiological parameters for concurrent studies. Additional blood samples were collected at each 30, 60, and 90 min post-injection of tritium for body water analysis, as described by Shero et al. (2014). Total blood volume collected for each animal was limited to less than 0.7 % of total animal blood volume. Blood serum was isolated by centrifugation 2 to 10 h following collection and frozen and stored at −80 °C prior to analysis.

2.3. Hormone and binding protein assays

Circulating blood hormone concentrations (cortisol, GH, IGF-I, tT_4, fT_4, and tT_3) were measured using ^{125}I radioimmunoassays validated for use with Weddell seal serum. Commercial kit assays were used for tT_4 (tT_4; IVD Technologies, TT_4-1000 V, Santa Ana, CA), tT_3 (tT_3; IVD Technologies, TT_3-1000 V), fT_4 (fT_4; IVD Technologies, FT4–2000 V; included equilibrium dialysis step), and cortisol (MP Biomedical 06B-256440, Irvine, CA). Parallelism and accuracy tests were used to validate all hormone assay kits for use with Weddell seal serum (details in Supplementary Figs. 1 and 2). Serum concentrations of IGF-I and GH were measured in a subset of samples (n = 102 for GH and n = 125 for IGF-I) using heterologous in-house (non-commercial) radioimmunoassays previously validated for Weddell seal sera (Shero et al., 2015) and originally described in Richmond and Zinn (2009). Inter- and intra-assay coefficient of variation (CV) were quantified using a Weddell seal serum pool run with each assay batch. Interassay and intraassay CV were within acceptable ranges: tT_4 (8 %, 9 %), tT_3 (9 %, 12 %), fT_4 (7 %, 11 %), cortisol (6 %, 7 %), IGF-I (16 %, 4 %), and GH (8 %, 8 %), respectively.

Serum IGFBP-2 and IGFBP-3 were quantified in a representative subset of Weddell seals (n = 33) by Western ligand blot, as described by Richmond et al. (2010a). Briefly, proteins were separated by polyacrylamide gel electrophoresis and transferred to a nitrocellulose membrane that was incubated with ^{125}I-labeled human IGF-I (Amersham Pharmacia Biotech, Piscataway, NJ), washed to remove unbound ligand, and exposed to a phosphor screen (Packard Instrument Company, Meriden, CT) so that bound radioactivity could be quantified using ImageQuant TL software (Cytiva Life Sciences, USA). A pooled Weddell seal serum sample was included in each gel along with study animal samples. IGFBP

concentrations were quantified as the percentage of digital light units (pixels per mm^2) in each sample band relative to the digital light units for the Weddell seal pool band.

All hormone analyses were performed using serum samples from the initial collection of blood (collected approximately 10 min after initial injection of sedatives, prior to weighing), with the exception of GH and IGF-I assays, which used serum collected 30–60 min later (extra serum from body water analysis) due to limited quantities of available serum.

2.4. Weaning and mass recovery calculations

Because postpartum females were handled late in lactation but prior to weaning, mass loss continued for several days beyond initial body mass measurement. Therefore, to predict post-weaning mass recovery rates, it was necessary to estimate the date of weaning and the amount of body mass lost between time of data collection and weaning. For all postpartum females sampled in early summer that had known parturition dates (n = 56; 8 postpartum females had uncertain parturition dates due to disruption of colony surveys in 2013), each female's mass at parturition (kg) was estimated using Wheatley et al.'s (2006) average rate of daily mass loss during lactation (10.53 $g \cdot kg^{-1}.day^{-1}$ calculated by combining data from two seasons) and DPP at the time of initial handling:

$$\text{Mass}_{\text{postpartum}} = \frac{\text{Mass}_{\text{handling}}}{1 - (0.01053 \cdot \text{DPP})}$$

Individual mass loss rates throughout lactation were calculated as the product of each female's mass at parturition and the 10.53 $g \cdot kg^{-1}.day^{-1}$ rate, averaging 4.68 $kg \cdot day^{-1}$ (range: 3.62–6.43 $kg \cdot day^{-1}$). The total duration of lactation for each female was estimated based on the assumption that females weighing less than 355 kg on the day of pupping had a lactation duration of 33 days (n = 4 females in this study), while those heavier than 355 kg nursed their pups for proportionally longer periods (Wheatley et al., 2006):

$$\text{Duration}_{\text{lactation}} = 0.07 \cdot \text{Mass}_{\text{postpartum}} + 6.98$$

For 10 females in this study, the predicted weaning date occurred prior to initial sampling. Since all females still had attendant pups, lactation durations for these females were adjusted to one day after sampling (i.e., if $\text{Duration}_{\text{lactation}} - \text{DPP}$ was < 1, $\text{Duration}_{\text{lactation}}$ was reassigned as DPP + 1).

Female body mass at pup weaning was predicted by applying each female's estimated rate of mass loss during lactation to the total number of days between sampling date and predicted weaning date. Predicted weaning mass and weaning date were then used to calculate post-lactation mass change rates on both an absolute ($kg \cdot day^{-1}$) and mass-specific ($g \cdot kg^{-1}.day^{-1}$) scale for females that were rehandled in late summer after a recovery period. Overall summer mass change rates were also calculated for all seals that were handled twice on an absolute scale (difference in mass between the early and late summer sampling dates divided by the total number of days between samplings), as well as on a mass-specific scale (overall mass change rate divided by mass at early summer sampling).

2.5. Statistical methods

All statistical analyses were completed using Rstudio and R version 4.1.0 (R Core Team, 2019), and significance was assessed at $p < 0.05$. Values are presented as mean ± standard deviation unless otherwise noted. For analyses applying an information criterion approach, models were ranked based on Akaike's information criterion corrected for small sample size (AICc). When a single top model was selected, additional factors were maintained only if they lowered AICc by at least 2, and to prevent overfitting, models included no more than one predictive variable for every ten animals used to fit the model. Mixed effects models were fitted using R packages *lme4* (Bates et al., 2015) and *mgcv* (Wood, 2011). For response variables with a right-skewed distribution, models were fitted as generalized linear models using a gamma distribution and log link functions. Residuals for all top models were examined for patterns and high leverage data points to confirm proper fits.

To characterize categorical differences in body mass, percent lipid, mass change rates, and serum hormone and IGFBP concentrations between reproductive groups (postpartum and skip females) and seasons (early summer and late summer), generalized linear mixed-effects models were developed. Individual animal ID was treated as a random effect, and post-hoc Tukey's HSD tests were used to make comparisons among groups and seasons.

To determine how body mass and percent lipid in postpartum and skip females were associated with animal age, standard length, season, date of sampling, and birth timing (parturition date and DPP in postpartum females), we applied an AICc-based model comparison approach. Separate suites of models were developed for postpartum females and skip females, which were compared by AICc to identify the strongest predictive variables for each group. We examined models including all factors plus interactions between season and other variables. All models included an animal ID random effect. For postpartum females, significant seasonal interaction effects were identified, so separate models were developed for early summer and late summer.

To test whether circulating hormone concentrations were most strongly associated with body mass, season, reproductive group, and/or lactation status, a similar AICc-based approach was used. Lactation status reflected whether an animal was lactating when handled, i.e., was a postpartum female handled in early summer, and was not considered in models that included season or reproductive group as separate factors to avoid confounding effects. Interactions between season and reproductive group and between body mass and the other variables were tested as factors, and a random effect for animal ID was included in all models. A separate suite of thyroid hormone models that included tT_4 as a predictor was used to test for relationships between tT_4, fT_4 and tT_3, and other factors.

To determine whether circulating hormone concentrations or changes in hormone concentrations across summer were linked to body mass gains and losses, we developed linear models that predicted body mass change rates in postpartum and skip females separately and compared models by AICc. For skip females, models included hormone concentrations (cortisol, GH, IGF-I, tT_4, tT_3, and fT_4, and fT_4:tT_4 and tT_3: tT_4 ratios) during early and late summer, changes in hormone concentrations over summer (i.e., late summer hormone concentration minus early summer concentration), and age as predictive variables.

For postpartum females, we tested all the same factors in relation to post-weaning mass gain rates except for early summer hormone concentrations, which we excluded because these values were more likely to reflect lactational physiology, not mass recovery. Since serum GH and IGF-I were only measured in a subset of animals, candidate models including these factors were assessed first, and then models without GH and IGF-I data were fitted with a larger sample size.

3. Results

3.1. Body mass and composition dynamics

Postpartum and skip females' changes in body mass and percent lipid between early and late summer were effectively opposite (Fig. 2, Table 1). While skip females were larger and had significantly greater body fat percentages than postpartum females at both time-points, skip females lost 1.03 ± 0.35 kg·day^{-1} (mostly lipid) across the summer (Table 1). In contrast, postpartum females gained 0.60 ± 0.57 kg·day^{-1} between samplings, gaining mass after the predicted date of weaning at the higher estimated rate of 0.98 ± 0.56 kg·day^{-1} (averaging gains of 0.36 % of body mass at weaning per day). Postpartum mass gains were disproportionately lean mass, as average total lipid mass and percent lipid declined across the summer (Table 1). Despite their high rate of mass gain, postpartum females were still significantly lighter (65 kg lower average body mass) and leaner (8.3 % lower mean percent lipid) than skip females in late summer (Table 1; Tukey HSD, $p < 0.0001$).

Total body mass of skip females was best predicted by standard length of the animal ($F_{1,20} = 10.837$, $p = 0.0036$) and the season of sampling (early versus late summer) ($F_{1,20} = 143.560$, $p < 0.0001$), while percent lipid varied only with season ($F_{1,19} = 34.821$, $p < 0.0001$) (Table 2). In postpartum females, the factors that best predicted body mass and percent lipid differed by season. During early summer, the heaviest postpartum females were the longest ($F_{1,52} = 40.658$, $p < 0.0001$) and had earlier pupping dates ($F_{1,52} = 8.709$, $p = 0.0047$). During late summer, postpartum females that were older ($F_{1,47} = 4.287$, $p = 0.0439$), longer ($F_{1,47} = 28.643$, $p < 0.0001$), and sampled later after birth (i.e., at greater DPP) ($F_{1,47} = 20.216$, $p < 0.0001$) were heavier. Postpartum seals sampled at greater DPP had lower body percent lipid during both early summer ($F_{1,53} = 15.001$, $p = 0.0003$), when they had presumably lost more fat while nursing, and during late summer ($F_{1,49} = 20.15$, $p < 0.0001$), when they had had more time post-weaning to recover lean mass (Table 1).

3.2. Endocrine dynamics

Serum concentrations of metabolic hormones were linked to body mass, season, or whether an animal was currently lactating or non-lactating and differed between postpartum and skip females (Table 3, Fig. 3, Fig. 4). For example, circulating cortisol concentrations were similar between postpartum and skip females in early summer (despite greater body masses of skip females) and increased across summer in both groups ($F_{1,136} = 210.2$, $p < 0.0001$); however, the increase was more pronounced in postpartum seals (Fig. 3A). Overall, models indicated that circulating cortisol levels were better predicted by season, reproductive group, and their interaction than by body mass or percent lipid (Table 3, Fig. 4A). In contrast, serum GH concentrations were greater in females with lower body masses ($F_{1,69} = 54.07$,

$p < 0.0001$). Postpartum females thus had greater circulating GH concentrations compared with skip females in both early and late summer (Fig. 3B, Fig. 4B). Even with controlling for the effect of body mass, serum GH was greater in postpartum females compared with skip females ($F_{1,69} = 18.11$, $p < 0.0001$). Circulating GH also was more steeply negatively correlated with mass in postpartum seals than in skip females, reflecting a significant mass:reproductive group interaction effect ($F_{1,69} = 15.29$, $p = 0.0002$) (Table 3). Serum concentrations of IGF-I and IGFBP-3 were positively correlated with body mass (IGF-I: $F_{1,114} = 47.78$, $p < 0.0001$; IFGBP-3: $F_{1,31} = 4.29$, $p = 0.0468$), while IGFBP-2, like GH, was negatively correlated with mass ($F_{1,30} = 9.84$, $p = 0.0038$) (Fig. 4C–E, Table 3). Lactating females had lower mean serum concentrations of IGF-I and IGFBP-3 and higher concentrations of IGFBP-2 as compared to non-lactating females (postpartum females in late summer and skip females in both seasons) (Fig. 3C–E). Lactating females also had greater levels of IGFBP-2 ($F_{1,30} = 25.21$, $p < 0.0001$) relative to their body masses than non-lactating females (Table 3, Fig. 4D).

Concentrations of the thyroid hormones (tT_4, fT_4, and tT_3) in postpartum and skip females also indicated altered dynamics during lactation (Table 3). Lactating seals had the lowest mean serum concentrations of tT_4 and fT_4 and the greatest concentrations of tT_3 (Fig. 3F–H), resulting in the highest tT_3:tT_4 and fT_4:tT_4 ratios. While there was a positive correlation between serum tT_4 and mass across all samples ($F_{1,147} = 15.28$, $p = 0.0001$) (Fig. 4F), lactating females had lower tT_4 for a given body mass ($F_{1,147} = 31.30$, $p < 0.0001$). Serum concentrations of fT_4 and tT_3 were not predicted by mass but were predicted by tT4 (fT4: F1,136 = 137.6, $p < 0.0001$; tT3: F1,118 = 91.39, $p < 0.0001$), with lactating females having higher relative fT_4 and tT_3 concentrations compared with non-lactating seals (fT_4: $F_{1,136} = 9.85$, $p = 0.0002$; tT3: F1,118 = 91.48, $p < 0.0001$) (Fig. 5).

3.3. Links between hormones and mass changes

Testing whether serum hormone concentrations or their changes over summer were linked to body mass gains or losses revealed different associations in postpartum and skip females. In postpartum seals, among the relatively small sample of females (n = 18) for which parturition date and serum GH concentrations in both handling periods were known, a greater decline in GH over summer predicted a higher rate of mass gain after weaning ($F_{1,16} = 9.727$, $p = 0.0066$) (Table 4, Supplementary Fig. 3). Within the full sample of twice-handled postpartum females with known parturition dates (n = 37) (including some animals missing GH or IGF-I measurements), animal age was the sole predictor of post-weaning mass gain ($F_{1,35} = 9.996$, $p = 0.0032$), as older postpartum seals recovered body mass more quickly (Fig. 6). In skip females, the rate of body mass loss across summer was not linked to age or serum GH concentrations, but skip females with higher T_3 in the breeding period lost mass across summer at a greater rate ($F_{1,21} = 5.289$, $p = 0.032$).

4. Discussion

Postpartum mass recovery in seals and its endocrine regulation is not well understood, despite this recovery being critical for foraging efficiency and thermoregulation, especially in highly seasonal polar environments. This study of Weddell seal mass changes revealed

that postpartum female seals replenish mass rapidly between early and late summer following lactation weight loss. In contrast, skip female Weddell seals lost mass between early and late summer, suggesting they do not need to maintain large body masses across this time. These opposing mass change patterns were also reflected in endocrine dynamics, as serum concentrations of cortisol, GH, IGF-I, IGFBP-2 and −3, and thyroid hormones all differed between postpartum and skip females in early and/or late summer, mostly in ways consistent with our predictions. Relationships between these hormones and body mass suggest how stores of fat and protein are regulated in a mammal that undergoes seasonal, energetically costly life history events.

4.1. Postpartum females

Summer foraging by postpartum females resulted in mass recovery at rates nearly five times higher than the average rate of mass gain during the winter (1.0 $kg \cdot day^{-1}$ November to February versus 0.2 $kg \cdot day^{-1}$ February to October (Shero et al., 2015)). Rapid post-weaning, summer mass gains in Weddell seals are likely supported by the seasonal availability of prey at shallow depths and constant daylight that facilitates visual foraging (Beltran et al., 2021; Davis et al., 1999). Postpartum females gained lean mass rather than lipid mass during their midsummer (November to February) foraging period, fully restoring their total protein stores to amounts seen in seals shortly after birth (Wheatley et al., 2006). Indeed, by late summer, total lean mass values were similar (i.e., not significantly different) between the postpartum and skip female groups. Therefore, Weddell seals fit a pattern observed in many mammalian species of prioritizing lean tissue repletion before lipid accumulation (Byers, 1982; Chan-McLeod et al., 1994; Keogh et al., 2015b; Sheriff et al., 2013; Skiba, 2010). This suggests Weddell seals maintain enough lipid through lactation for sufficient thermoregulation in the warmer summer months and do not need to immediately deposit blubber post-weaning. Regaining lean mass early in the post-weaning period may reduce atrophy or loss of swimming muscle fibers (Hindle et al., 2009; Rehfeldt et al., 1999) or digestive organ mass (Hume et al., 2002; Piersma and Lindström, 1997), thereby sustaining foraging and energy uptake abilities needed to facilitate later gains in both lipid and lean mass. Foraging success also appears to be related to experience, as older postpartum female seals (within the study animal age range of 10 to 20 years) gained mass at faster rates than fully grown younger individuals.

Circulating concentrations of somatotropic hormones (GH, IGF-I, and IGFBP-2 and −3), cortisol, and thyroid hormones all likely contributed to successful lactation and subsequent lean mass gains in postpartum Weddell seals. GH stimulates milk synthesis in mammals via multiple mechanisms, including by supporting uptake and use of nutrients for milk production and by increasing the release of IGF-I (Etherton and Bauman, 1998). The high serum concentrations of GH in lactating postpartum Weddell seals probably supported milk synthesis as well as protein sparing, helping minimize loss of protein for energy production even as lactating females lost lean mass in order to provision pups with amino acids in milk (Champagne et al. 2012). Postpartum seals' relatively high levels of circulating GH later in summer likely facilitated rapid lean tissue accretion post-weaning, given the stimulatory effects of GH on lipolysis, reduced protein turnover rates, and protein anabolism (Breier, 1999; Carter-Su et al., 1996; Eigenmann et al., 1985; Kersten, 2001; Møller et al., 2003).

Across summer, GH levels declined the most in postpartum seals with the highest rates of mass gain, likely disinhibiting fat accumulation and allowing a transition from protein to lipid recovery (Hayden et al., 1993). The negative relationship observed between GH and body mass suggests that large female Weddell seals, particularly those over 400 kg, had sufficient protein stores and could prioritize accruing fat. Conversely, maintaining highly elevated GH concentrations to support lean mass recovery appears to be important in postpartum seals that recovered mass at slower rates and retained low body masses (e.g., <300 kg) months after weaning. GH patterns in postpartum Weddell seals recovering lost mass were consistent with repletion in harbor seal pups (*Phoca vitulina*), northern elephant seal (*Mirounga angustirostris*) yearlings, and juvenile Steller sea lions (*Eumetopias jubatus*), where circulating GH declined as mass was recovered following extended periods of natural fasting or experimental periods of food restriction (Dailey et al., 2016; Dailey et al., 2020; Richmond et al., 2010a).

Lactating Weddell seals in this study sampled at approximately 35 DPP had relatively low serum concentrations of IGF-I, as did Weddell seals sampled in early lactation in a separate study (~5 DPP) (Shero et al., 2015). Lowered circulating IGF-I levels during lactation have been reported in other species (Cohick, 1998; Vega et al., 1991; Travers et al. 1993), and in Weddell seals, these low levels are likely the result of the negative feedback of nutritional restriction (i.e., reduced foraging) on GH-triggered IGF-I release from the liver (Breier, 1999; Keogh et al., 2015a; Straus and Takemoto, 1990). Since elevated IGF-I suppresses protein catabolism, low IGF-I throughout lactation in Weddell seal females likely supports a shift from an anabolic state during late-stage pregnancy to a catabolic state where somatic stores are mobilized to support milk production (Velloso, 2008). Once female Weddell seals weaned their pups and resumed feeding more and regaining mass, GH likely stimulated IGF-I release that promoted protein anabolism (Estívariz and Ziegler, 1997; Laron, 2001; Nordstrom et al. 2011). Low IGF-I concentrations during nutritional restriction and elevated concentrations during realimentation have been documented in other pinnipeds (Dailey et al., 2020; du Dot et al., 2009; Richmond et al., 2010a). Findings in this study similarly suggest IGF-I plays a critical role in energy conservation and mass recovery in Weddell seals.

The impact of circulating IGF-I on metabolism in lactating and post-weaning Weddell seals was almost certainly influenced by serum levels of IGF binding proteins that generally increase (e.g., IGFBP-3) or decrease (e.g., IGFBP-2) IGF-I bioavailability and affect target tissue specificity (Bach, 2018; Breier, 1999). Lactating female Weddell seals had the highest serum IGFBP-2 concentrations and lowest IGFBP-3 concentrations of all seals in this study, which presumably decreased the receptor signaling activity of already low circulating IGF-I levels in somatic tissue (Clemmons and Underwood, 1991). This reduced signaling likely facilitated lean tissue catabolism and amino acid mobilization for milk protein synthesis (Breier, 1999; Rehfeldt et al., 2010). IGFBP levels likely also had impacts on milk synthesis through local effects on IGF-I transport and signaling in mammary glands, as seen in studies of IGFBP dynamics in lactating domestic species (Cohick, 1998; Ha et al., 2016; Prosser and Schwander, 1996). After postpartum seals weaned their pups, their serum IGFBP-2 declined and IGFBP-3 increased while they rapidly and preferentially accreted lean tissue mass. These patterns are consistent with each binding protein's known responses

to nutritional intake and impacts on IGF-I activity and muscle growth (Clemmons and Underwood, 1991), as well as with IGFBP patterns in harbor seal pups recovering mass and in domestic species after weaning (Ha et al., 2016; Richmond et al., 2010b).

Serum cortisol concentrations also appear to play a role in regulating Weddell seal lean mass dynamics during both lactation and recovery. Serum glucocorticoid levels generally increase in animals with limited food intake (Secor and Carey, 2016), and circulating cortisol increases during lactation in several domestic mammal species, potentially to support milk synthesis by increasing energy sources available in circulation and through impacts to gene expression in the mammary gland (Stead et al., 2022). In free ranging pinnipeds, serum cortisol concentrations have been shown to rise during natural periods of negative energy balance, including lactation (Champagne et al., 2006; Di Poi et al., 2015; Fowler et al., 2016; Guinet et al., 2004; Ortiz et al., 2001). We did not observe elevated levels of circulating cortisol late in lactation as we predicted we would, as late lactation cortisol levels were similar to those reported at 5 DPP (Shero et al., 2015). Low serum cortisol throughout pinniped lactation may prevent excessive protein catabolism (Bennett et al., 2013; Crocker et al., 2012). It could also sustain maternal attendance to pups, as elevated cortisol may act as a re-feeding signal prompting females to leave nursing offspring (Guinet et al., 2004). In addition, because high cortisol concentrations can inhibit estrus and ovulation (Bronson, 1989; Tilbrook et al., 2000), lower cortisol levels in late lactation may facilitate breeding. Between early and late summer, after female Weddell seals in this study mated and weaned their pups, their serum cortisol levels increased, as did foraging activity and mass gain (Beltran et al., 2021). While elevated circulating cortisol generally stimulates both lipolysis and proteolysis, the proteolytic effects of glucocorticoids may be reduced when GH concentrations are also elevated (Douyon and Schteingart, 2002; Horber and Haymond, 1990). Thus, high serum GH concentrations in postpartum females may have reduced protein catabolism after weaning, while additive lipolytic effects of serum cortisol and GH promoted lean mass accretion (Djurhuus et al., 2004).

Thyroid hormone patterns in postpartum seals also likely regulated body stores during lactation and across summer, given the important roles of T_4 and T_3 in modulating energy expenditure at organismal and tissue-specific levels (Brent, 2012). Across species, serum thyroid hormones during lactation generally stimulate milk production, but circulating concentrations of T_4 and T_3 vary and sometimes decrease while rates of T_4 conversion to T_3 within the mammary gland increase (Tucker, 2000). The low serum tT_4 concentrations of lactating Weddell seals sampled in this study probably reflected their low food intake and depleted body condition and may have helped lower metabolic rate in most tissues to conserve energy (Eales, 1988). The high serum concentrations of tT_3 and tT_3:tT_4 and fT4:tT4 ratios seen in lactating versus non-lactating seals in this study likely supported milk synthesis by enhancing nutrient availability and partitioning to the mammary gland (Josefson et al., 2024). After weaning, serum tT_3 concentrations decreased and tT_4 increased in postpartum Weddell seals in this study. Post-weaning elevation of tT_4 occurs in other mammals (Benjaminsen, 1981; Wilsterman et al., 2015), and it likely stimulates mass gain in Weddell seals by promoting food intake and supporting protein anabolism (Alva-Sánchez et al., 2012; Flaim et al., 1978; Macari et al., 1986). Increases in tT_4 between early summer

and late summer in Weddell seals may also support successful hair cycling (molt) and establishment and maintenance of pregnancy (Colicchia et al., 2014; van Beek et al., 2008).

4.2. Skip females

Skip females demonstrated very different mass and endocrine dynamics than postpartum Weddell seals. Prior work has shown that at the start of spring (October), skip females and postpartum Weddell seals that have just given birth have similar body masses and percent lipid (Shero et al., 2015); however, lactating females lose mass rapidly (about 4 $kg \cdot day^{-1}$) (Wheatley et al., 2006) and become leaner prior to initiating mass recovery after weaning (discussed above). In contrast, skip females in this study lost mass at a rate of about 1 $kg \cdot day^{-1}$ across the entire summer period, despite continued diving and foraging (Beltran et al., 2021). As a result, the difference in body mass and percent lipid between the larger skip females and leaner postpartum females decreased substantially between the end of lactation and late summer. Skip females also showed more stable hormone concentrations than postpartum seals—cortisol was the only hormone that increased across the measurement interval (Fig. 3A). There were numerous significant differences in circulating hormone concentrations between skip and postpartum females, but perhaps the most striking difference was skip females' much lower serum GH in both early and late summer, which likely played an important role in body mass patterns.

The distinct summer mass dynamics of postpartum and skip female Weddell seals can be understood within the framework of seasonal body mass "set points" (Mrosovsky and Fisher, 1970). Many studies have found that target masses of animals vary seasonally, often in response to photoperiod, and that these set points then influence foraging activities, metabolic rate, and mass flux (Mercer, 1998; Morgan and Mercer, 2001; Rosen et al., 2021). Since postpartum and skip females experience the same environmental cues across the winter, they likely share a spring body mass set point targeting a body size large enough to fuel lactation. However, in skip females, the very large fat stores they accrue by spring are not needed to support nursing pups. Maintaining such large energy reserves across summer apparently is not a priority, given that all skip females lost mass during this timeframe. Metabolic hormones did not prevent this fat loss from occurring; rather, patterns in hormones seem optimized to support lean mass recovery in postpartum Weddell seals and may incidentally contribute to skip females losing mass. For example, the seasonal increase in cortisol observed in all Weddell seals in this study is likely important for stimulating foraging and promoting lean mass prioritization in postpartum females, but in skip females with large body masses and low circulating GH, elevations in cortisol could facilitate mass loss (Arlt and Stewart, 2005). Overall, low serum GH concentrations in skip females, along with reduced foraging (Beltran et al., 2021), likely caused skip females to consistently lose body mass across summer at a rate that is incidentally about the same as the rate at which postpartum seals gained mass. This may ultimately drive body masses of skip females towards a "lean and fit" late summer set point that is approximately the body mass postpartum females can achieve through intensive foraging post-weaning (Schultner et al., 2013). The fact that skip females can "afford" to forage less and lose mass over summer may confer advantages like accelerated molt or a higher rate of future reproductive success (Beltran et al., 2019).

5. Conclusions

This study revealed significant differences in summer mass and hormone dynamics in female Weddell seals tied to reproductive status. As predicted, postpartum Weddell seals that lost substantial mass during lactation regained lean mass at a rapid rate following weaning, likely due in part to elevated serum concentrations of GH, IGF-I, and IGFBP-3 and reduced serum IGFBP-2 concentrations later in summer. Postpartum seals' prioritization of lean mass recovery resulted in a decline in body percent lipid, highlighting that fat stores are not the sole indicator of nutritional status for Weddell seals and other species. Similarly, cortisol concentrations, which are often interpreted as indicators of nutritional stress, were not correlated with body mass or body mass change in either postpartum or skip females. Serum GH, however, may be a useful nutritional biomarker in Weddell seals and other pinnipeds given its strong negative correlation with body mass and apparent link to lean mass recovery. Total body stores, energy balance, and seasonal mass set-point dynamics likely all impacted metabolic hormone concentrations. Results from this study illustrate the important roles of metabolic hormones in mediating changes in lean tissue and lipid body stores associated with lactation and weaning.

Our findings in Weddell seals provide context for understanding seasonal physiology and energy dynamics in other species, including other pinnipeds. While Weddell seals forage intermittently during lactation, some pinniped species are fully capital breeders that fast throughout the pup attendance period (e.g., elephant seals), and others forage regularly and maintain high energy intake while nursing (e.g., otariid species). Weddell seals represent an interesting intermediate, and they also experience extreme seasonal fluctuations in foraging conditions. Future work may examine how post-weaning hormone patterns in other species (i.e., species that utilize different breeding systems or that face less seasonal variation in food availability) compare to those reported here, shedding further light on relationships between metabolic hormones, energy supplies and demands, and body mass changes.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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Data availability

Data generated in this study have been deposited and made publicly available through the Antarctic Master Directory, U.S. Antarctic Program (USAP) Data Center. Files are provided through the permanent link: https://www.usap-dc.org/view/dataset/601840.

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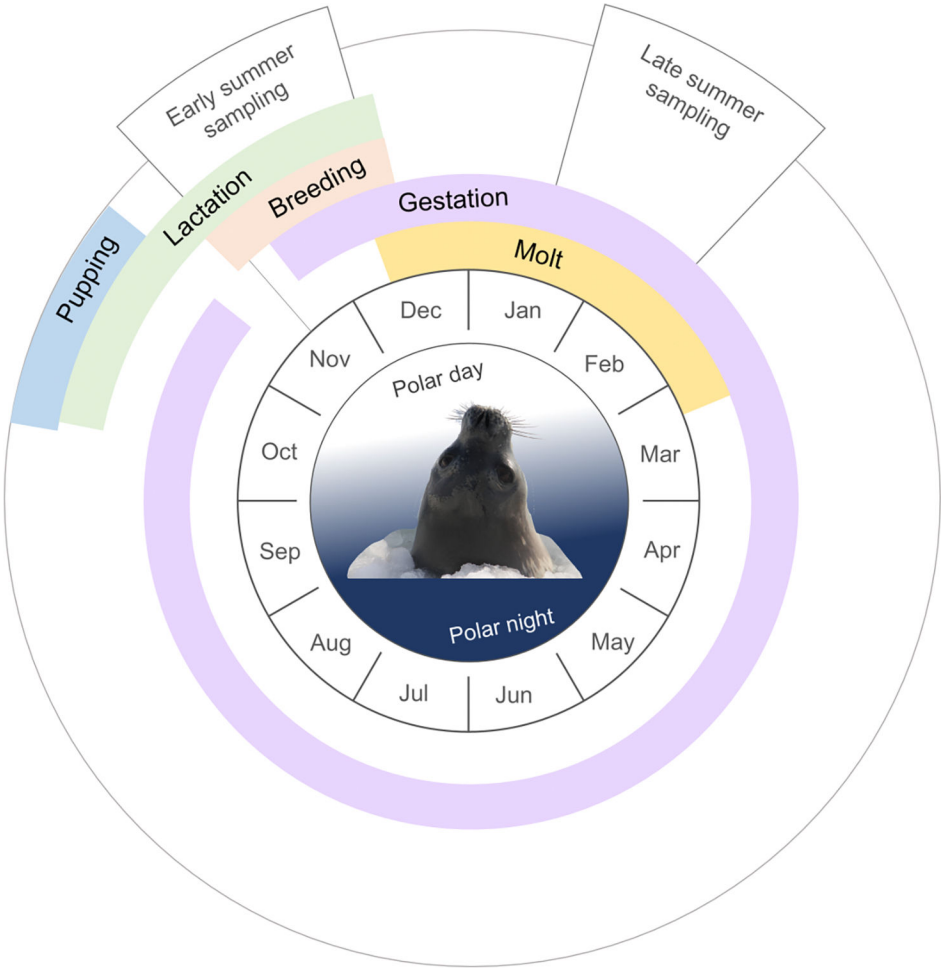

Fig. 1.

Diagram showing female Weddell seal annual life history timing at the population level and sampling windows for this study. During early summer, postpartum females were targeted for sampling at approximately 35 days postpartum, and females that did not pup in the current year (skip females) were handled at similar dates. Seals were sampled again in late summer, approximately 60 days after intial handling, during the period of annual molt and early gestation.

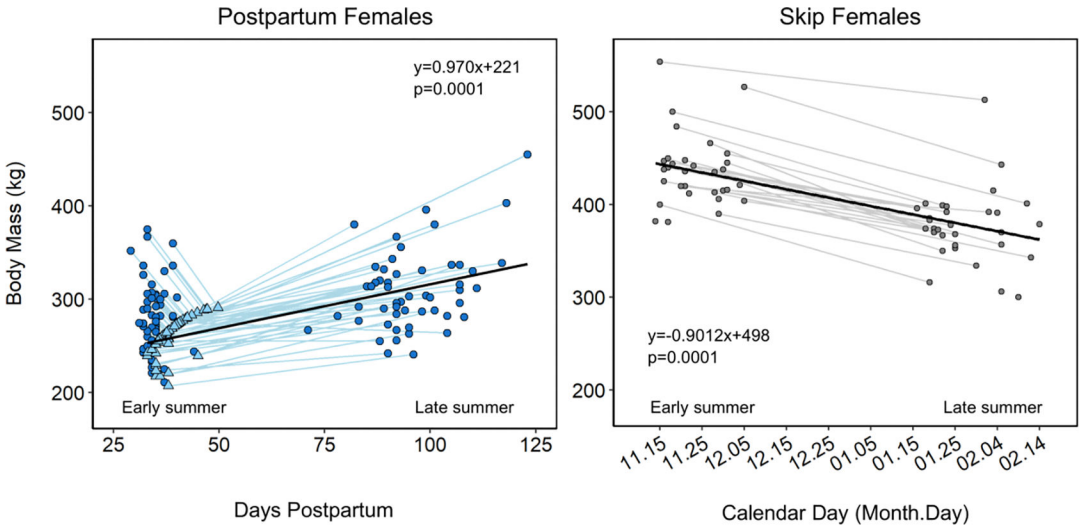

Fig. 2.

Patterns in body mass changes across austral summer in postpartum (blue) and skip (gray) female Weddell seals. For postpartum females, thin blue lines connect points for body mass measured (dark blue circles) in early summer (late lactation, approximately 35 DPP), estimated body mass at the predicted time of weaning (light blue triangles), and body mass measured in late summer (molt period, approximately 95 DPP) for individual seals. For skip females, thin lines connect body mass data points for individual seals handled in both the breeding period and late summer. Black lines, linear equations, and p-values reflect linear regressions for mass against DPP for postpartum females (regression excludes late lactation mass to reflect post-weaning mass recovery) and for mass against calendar day for skip females. The x axis for both panels reflects the same total number of days.

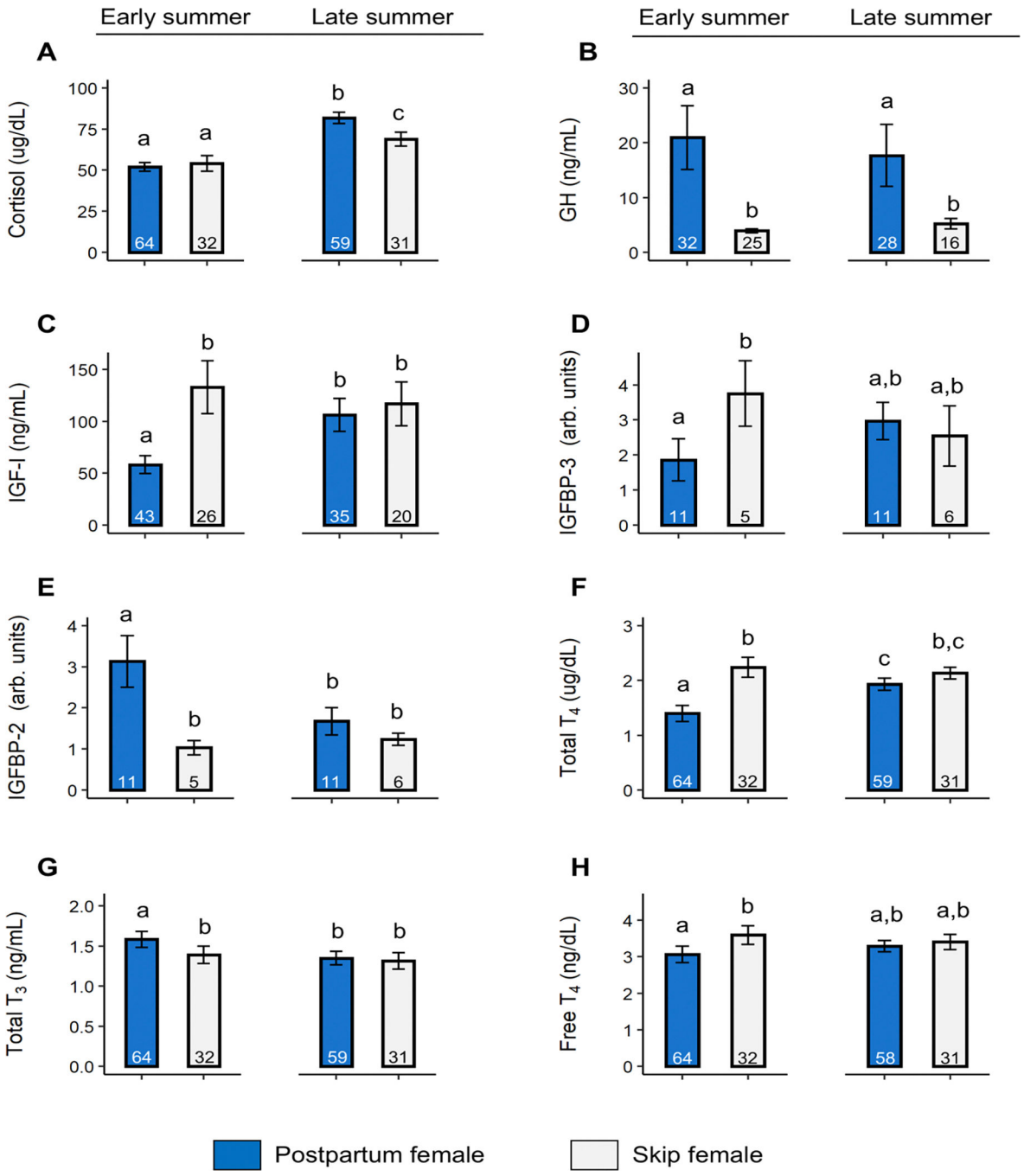

Fig. 3.

Serum concentrations of hormones (cortisol, growth hormone (GH), insulin-like growth factor-1 (IGF-I), total thyroxine (T_4), total triiodothyronine (T_3), and free T_4) and IGF binding proteins 2 and 3 (IGFBP-2 and IGFBP-3) in postpartum female and skip female Weddell seals. Concentrations of IGF binding proteins are in adjusted percentage of a gel standard quantified as digital light units per mm^2, referred to here as arbitrary (arb.) units. Error bars reflect 95 % confidence intervals. Samples sizes are shown at the base of each bar. Differences in concentrations between groups were tested by generalized linear mixed

effects models followed by Tukey's HSD, and letters represent significant differences ($p < 0.05$).

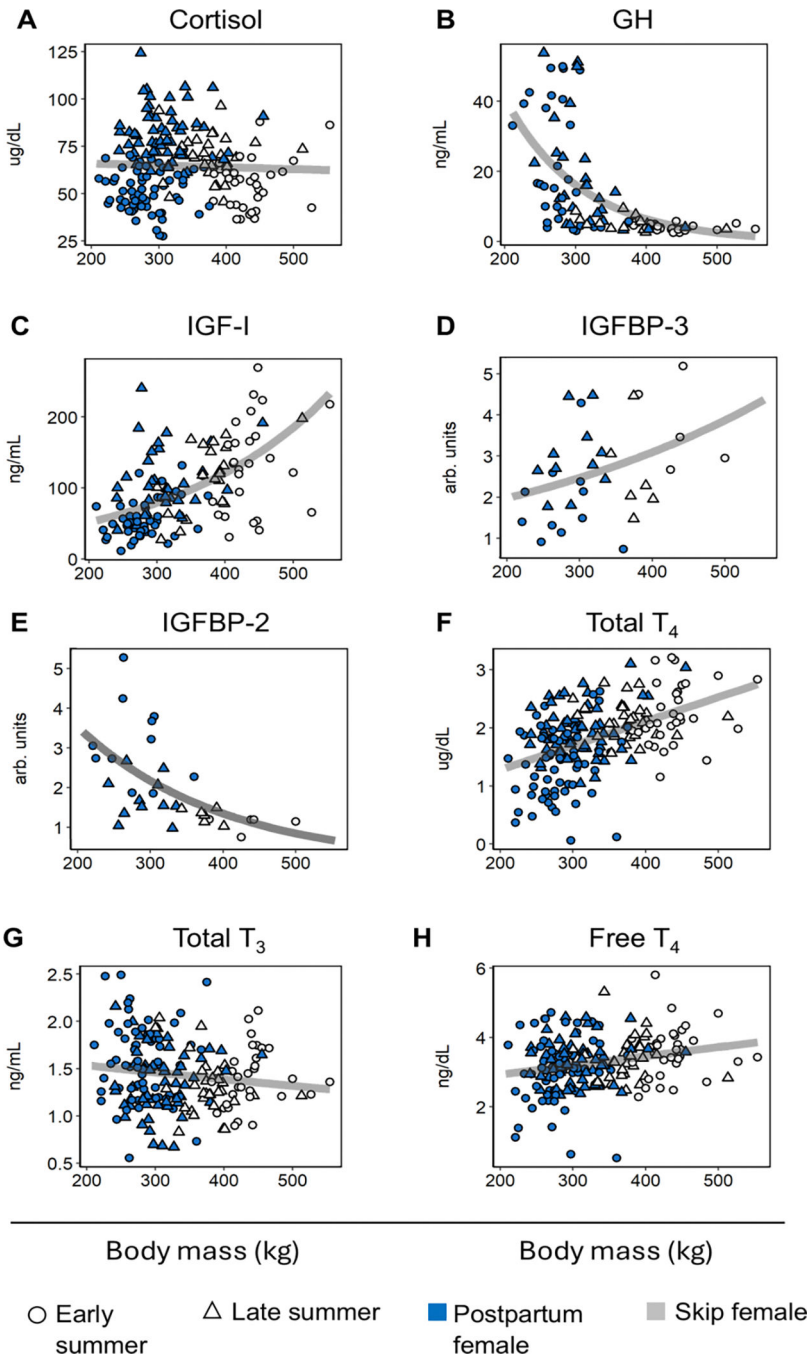

Fig. 4.

Serum concentrations of hormones (cortisol, growth hormone (GH), insulin-like growth factor-1 (IGF-I), total thyroxine (T_4), total triiodothyronine (T_3), and free T_4) and IGF binding proteins 2 and 3 (IGFBP-2 and IGFBP-3) in relation to body mass in postpartum female and skip female Weddell seals during the early summer (breeding period, November/December) and late summer (molt period, January/February). Concentrations of IGF binding proteins are in adjusted percentage of a gel standard quantified as digital light units per mm^2, referred to here as arbitrary (arb.) units. Gray lines reflect a linear regression (total T_4)

or fits from generalized linear models fitted with a gamma distribution and log-link (all other variables), and they illustrate the overall relationships between body mass and serum analyte concentrations.

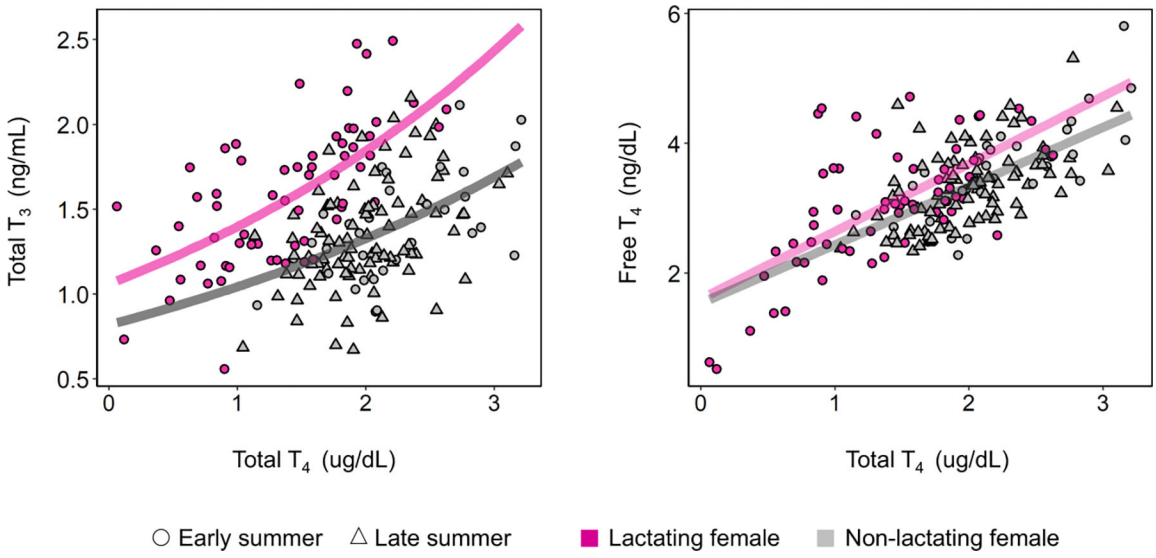

Fig. 5.

Serum concentrations of total triiodothyronine (T_3) and free thyroxine (T_4) in relation to serum total T_4 concentrations in all female Weddell seals. Relationships differed between lactating females (postpartum females handled in early summer) and non-lactating females (postpartum females handled in late summer, i.e., after weaning, and all skip females), and lines reflect generalized linear model fits (total T_3) or linear regressions (free T_4) between circulating hormone concentrations in each group.

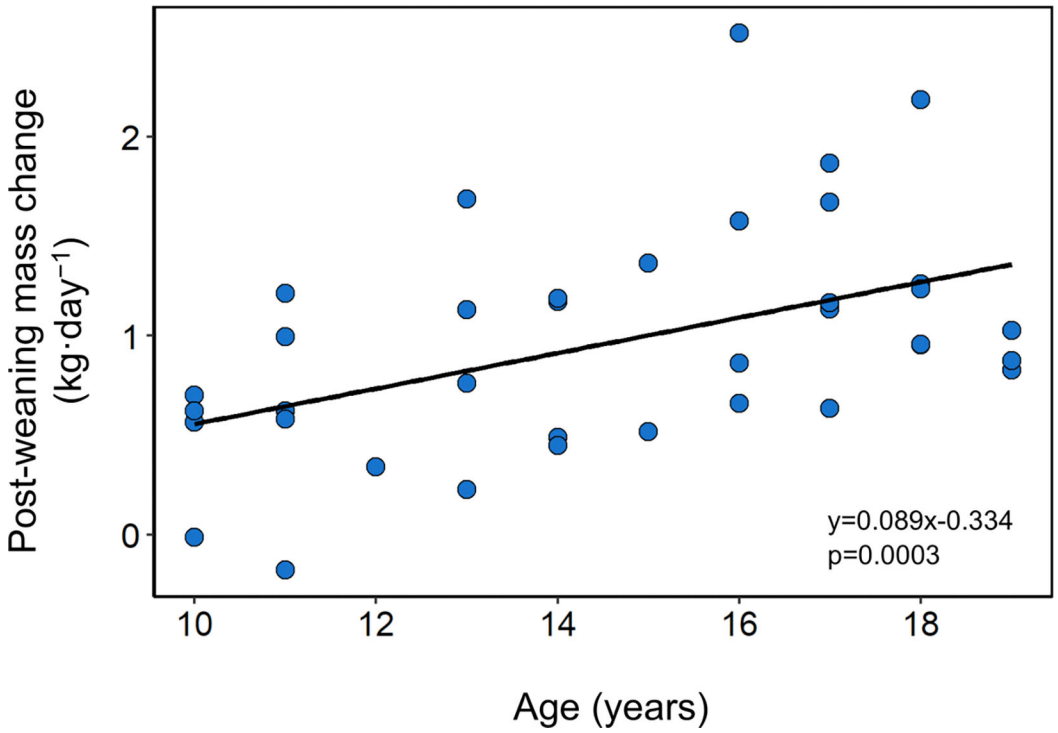

Fig. 6.

Mass gain rates of postpartum female Weddell seals between estimated weaning date (see Fig. 3) and late summer in relation to age. The black line, linear equation, and p-value reflects the associated linear regression.

Table 1

Summary of body mass and body condition parameters in female Weddell seals across the austral summer, beginning in early summer (lactation and breeding period, November/December) and ending in late summer (molt period, January/February). Values are means ± standard error. Letters represent significant differences between groups and sample sizes are shown in parentheses.

	Postpartum Females		**Skip Females**	
Season	**Early Summer**	**Late summer**	**Early Summer**	**Late summer**
Body mass (kg)	282 ± 5 ^{a} (63)	311 ± 6^{b} (58)	437 ± 7^{c} (31)	376 ± 7 ^{d} (32)
Percent lipid	31.8 ± 0.5 % ^{a} (62)	25.3 ± 0.5 % ^{b} (58)	38.2 ± 0.6 % ^{c} (30)	33.6 ± 0.6 % ^{a} (29)
Total lean mass (kg)	192 ± 3 ^{a} (62)	231 ± 4^{b} (58)	269 ± 5^{c} (30)	251 ± 5^{b} (29)
Total fat mass (kg)	90 ± 2 ^{a} (62)	79 ± 3^{b} (58)	166 ± 4^{c} (30)	126 ± 3 ^{d} (29)
Total protein mass (kg)	46 ± 1 ^{a} (62)	56 ± 1^{b} (58)	63 ± 1^{c} (30)	59 ± 1^{b,c} (29)
Daily Δ mass (kg·day^{-1})	–	0.60 ± 0.09 ^{a} (43)	–	−1.03 ± 0.07^{b} (23)
Daily Δ mass-specific mass (g·kg^{-1}day^{-1})	–	2.29 ± 0.32 ^{a} (43)	–	−2.318 ± 0.16^{b} (23)
Daily Δ mass post-weaning (kg·day^{-1})	–	0.98 ± 0.09 (37)	–	–
Daily Δ mass-specific mass post-weaning (g·kg^{-1}day^{-1})	–	3.55 ± 0.31 (37)	–	–
Daily Δ lean mass (kg·day^{-1})	–	0.74 ± 0.06 ^{a} (42)	–	−0.31 ± 0.08^{b} (20)
Daily Δ fat mass (kg·day^{-1})	–	−0.16 ± 0.06 ^{a} (42)	–	−0.72 ± 0.07^{b} (20)

Table 2

Top linear models predicting total body mass (kg) and percent lipid of female Weddell seals. The models for skip females are linear mixed-effect models (LMMs) which include both early summer (November/December) and late summer (January/February) season data and an animal ID random factor. The postpartum female models were developed separately for each period due to significant interaction factors with season. For the skip female LMMs, R^2 is the marginal R^2 value (fixed effects only). Fields with "–" indicate factors that were tested but not included in top models, and "n/a" reflects that a factor was not applicable to the sample group of the model. Season is a binary (dummy) variable with a value of 1 in Jan/Feb and 0 in Nov/Dec. DPP = days postpartum; K = number of factors.

	Group	Model coefficients							Model traits	
		intercept	age (yrs)	length (cm)	season	pup date	date	DPP	K	R^2
Body mass models	Skips, both periods (n=62)	−51.18	–-	1.948	−65.83	n/a	–-	n/a	2	0.62
	Postpartum, Nov/Dec (n = 56)	149.4	–-	2.171	n/a	−1.304	–-	–-	2	0.47
	Postpartum, Jan/Feb (n=51)	−363.5	4.293	1.779	n/a	–-	–-	1.874	3	0.53
Percent lipid models	Skips, both periods (n=59)	38.20	–-	–-	−4.66	n/a	–-	n/a	1	0.36
	Postpartum, Nov/Dec (n = 55)	49.96	–-	–-	n/a	–-	−0.234	–-	1	0.22
	Postpartum, Jan/Feb (n=51)	6.586	–-	–-	n/a	–-	–-	0.195	1	0.29

Table 3

Top generalized linear models predicting serum hormone (cortisol, insulin-like growth factor 1 (IGF-I), growth hormone (GH), total thyroxine (T_4), free T_4, and total triiodothyronine (T_3)) and circulating IGF-I binding protein 2 and 3 (IGFBP-2 and IGFBP-3) concentrations in female Weddell seals. K = number of fixed factors. R^2 is the adjusted R^2 calculated in the *mgvc* package (the proportion of variance explained, where unbiased estimators estimate original variance and residual variance). Samples sizes vary among hormones due to limited availability of serum for different assays.

Predictive factors tested	Serum Hormone	K	Link	Predictor variable(s)	R^2
Body mass, Season, Reproductive group, Lactation status, interactions	Cortisol (n=184)	3	Log	Season, Repro. group, Season: Repro.group	0.66
	Total T_4 (n=184)	2	Identity	Mass, Lactation	0.48
	IGF-I (n=123)	1	Log	Mass	0.31
	GH (n=100)	3	Log	Repro.group, Mass, Mass: Repro.group	0.57
	Total T_3 (n=184)	1	Log	Lactation	0.33
	Free T_4 (n=183)	1	Identity	Mass	0.24
	IGFBP-3 (n=33)	1	Log	Mass	0.09
	IGFBP-2 (n=33)	2	Log	Mass, Lactation	0.59
Total T_4, Season, Reproductive group, Lactation status, interactions	Total T_3 (n=184)	2	Log	Lactation, Total T_4	0.66
	Free T_4 (n=183)	2	Identity	Lactation, Total T_4	0.60

Table 4

Top linear models predicting over-summer body mass change rate (skip females) or post-weaning mass change rate (postpartum seals) in recaptured female Weddell seals. Predictive factors tested in candidate models included hormone concentrations (cortisol, GH, IGF-I, tT_4, tT_3, and fT_4) in both early and late summer (skip females) or only late summer (postpartum females), hormone over-summer change (i.e., late summer hormone concentration minus early summer concentration), fT_4:tT_4 and tT_3:tT_4 ratios during early and late summer, and age in years. Models were developed separately for postpartum and skip females and for the subsets of animals in which GH and IGF-I were measured and for the full, larger samples of recaptured seals.

Animal group	Predictive factors tested	Sample size	Predictor variable(s)	R^2
Postpartum females	All factors	18	GH.change	0.38
	All factors except GH and IGF-I parameters	37	age	0.22
Skip females	All factors	12	(null model)	n/a
	All factors except GH and IGF-I parameters	23	Early.summer.tT_3	0.20