Faculty of Biosciences, Fisheries and Economics

Department of Arctic and Marine Biology

Body composition changes of hooded seal (*Cystophora cristata*) pups during extreme lactation

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BIO-3950 Master's Thesis in Biology
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Photo by: Kristine Gonsholt

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Erling S. Nordøy, UiT — The Arctic University of Norway

Acknowledgements

This thesis would not have been what it is without the help of a few people.

First and foremost, I would like to thank my supervisor, Erling S. Nordøy, who gave me the chance to work in this amazing topic. I would also like to thank him for allowing me to work independently and thus giving me the chance to develop my skills and grow as a person.

I would also like to thank my family. To my mother, Ana Doris Guerrero, and my sister, Gracia Maria Guerrero, for their unconditional love and guidance. Especially, for always giving me encouragement and support to achieve my dreams.

Abstract

Among phocids, the hooded seal has the most extreme lactation period. It lasts, for most pups, four days, making it also the shortest lactation period of any mammal. During the lactation period, there is a high energy transfer, which affects and changes the body of the pup in preparation for the following post-weaning fast period. With regard to the decline of the West Ice population, the main purpose of this study was to examine the changes in the body composition and energy deposition of the West Ice pups during the lactation period, as well as the maternal strategy of the West Ice female hooded seals. In addition, energy deposition during pregnancy and during the lactation period over the last 10 years was investigated. From 2007 to 2018, as part of a series of student expeditions, newborn (*n*= 14) pups and weaned seals (*n*= 17) were captured in the West Ice. All pups (*n*= 31) were submitted to a detailed dissection for measurement of body composition. Energy deposition was assayed by chemical analysis for the last two weaned pups.

Body composition of newborn pups and weaned pups were significantly different. Newborn pups had a blubber content of 30.7 ± 2.9 %, while weaned pups had a body composition that was 46.6 ± 1.7 % blubber. During lactation, muscle mass increased by 23%, while blubber content increased by 63 %. Comparison of maternal strategies of the West Ice and Northwest Atlantic stock presented a significant difference, West Ice hooded seals appear to be born and weaned with greater deposits of blubber than hooded seals of the Northwest Atlantic population. Additionally, it seems that there has been a decline in the energy deposited by the female hooded seals into the weaned pups.

Keywords: Hooded seal newborn pups, Hooded seal weaned pups, *Cystophora cristata*, Body composition, Lactation period, Tissue growth, Post weaning fast, Energy density, Energy deposition, Maternal strategies, Climate change, Greenland Sea population decline

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1 Introduction

Pinnipeds are one of the three major clades of modern marine mammals and represent 28% of the diversity of marine mammals (Berta. et al., 2005). They are compromised by three monophyletic families, the Otariidae (eared seals or fur seals and sea lions), the Odobenidae (walruses), and the Phocidae (true or earless seals), which are the second major group of living seals (Berta. et al., 2005; Berta, 2017).

In the Arctic, phocids seals are well represented. Six phocids species that inhabit the Arctic are considered true arctic seals; the spotted seal (*Phoca largha*), ringed seal, (*Pusa hispida*), ribbon seal, (*Histriophoca fasciata*), harp seal (*Pagophilus groenlandicus*), bearded seal (*Erignathus barbatus*) and hooded seal (*Cystophora cristata*) (Blix, 2005).
These ice-breeding species are characterized by having long gestation periods plus delayed implantation and they all give birth on ice (ice floes or fast ice). After birth, the offspring grow a substantial blubber layer during an intense lactation period, which in these phocids can last from as short as 3 days to as long as 60 days. The lactation period is followed by an abrupt weaning when the pups are abandoned by their mothers (Oftedal et al., 1987; Oftedal et al., 1993; Boness and Bowen, 1996; Lydersen and Kovacs, 1999; Blix, 2005).

1.1 Hooded seals

Hooded seals, in particular, are markedly sexually dimorphic and one of the largest northern phocids. Adult males are around 2.5 m long and weigh on average from 200-300 kg, however, large males can reach 400 kg. Instead, adult females, weight around 150- 250 kg and have an average length of 2.2 m (Blix, 2005; Kovacs, 2018).

Their common name comes from their peculiar nasal ornament at the head of sexually matured males. During the breeding season, which is in late March, males inflate this nasal ornament as a display to females and other males. When it is inflated, it forms a bi-lobed "hood", covering the top of the head and the front of the face. Otherwise, when the nasal ornament is relaxed, it hangs as a wrinkled loose sac over the nose of the male. Besides the mating season, this hood appears to be used as a threat signal at other times of year (Blix, 2005; Kovacs, 2018).

Furthermore, these seals are also called bladdernose seal, due to the ability of adult males to expand their elastic nasal septum. They can blow it out through one of the nostrils as a big pink-red balloon, which is also used as a display to females and other male seals (Blix, 2005; Kovacs, 2018).

Hooded seals are considered a highly migratory, pelagic species (Folkow et al., 1996; Kovacs, 2018). They inhabit the deep waters of the North Atlantic and can be found in the ice filled arctic and subarctic waters. Currently, there are two recognized stocks, the Northwest Atlantic stock and the Greenland Sea stock (Northeast Atlantic stock). However, there are four breeding and whelping areas: in the Gulf of St. Lawrence, off southeastern Labrador (referred as “The Front”), in the Davis Strait (between Baffin Island and western Greenland) and in the West Ice (in the Greenland sea near Jan Mayen Island).The first three belong to the Northwest Atlantic stock, while the last one is the Greenland Sea stock (Sergeant, 1974; Bowen et al., 1985; Coltman et al., 2007; ICES, 2016; Kovacs, 2018).

1.1.1 Hooded seal pups

Hooded seal pups are born during late March and early April, very late during the pack ice season (Sergeant, 1974; Sergeant, 1976; Lydersen and Kovacs, 1999). Unlike, other phocids, hooded seals are born without lanugo, which it is shed in the utero (Oftedal et al., 1991). Therefore, pups are born with a short pelage which is blue on the back and silver on the belly, thus, hooded seal pups are also called “bluebacks”. This pelage is maintained until the first annual molting (Blix, 2005; Kovacs, 2018).

Aside from hooded seals and bearded seals, ice breeding phocids are born with a white lanugo. This fetal coat acts as an insulator when it is dry, as well as a heat trap for solar energy, which makes it critical in thermoregulation in neonates phocids. However, once it gets wet, it loses most of its thermoregulatory capabilities, which is the reason why newborns cannot tolerate getting into cold water (Oftedal et al., 1991; Lydersen and Kovacs, 1999). When wet, newborns may avoid hypothermia by burning brown adipose tissue (Grav and Blix, 1976). Hooded seal newborns, on the other hand, are born already with a thin subdermal layer of fat, that helps them in thermoregulation (Oftedal et al., 1991; Oftedal et al., 1993).

Briefly after parturition, pups start to suckle (Bowen, 1991). Hooded seal mothers remain on the ice floe the entire time with the pup until weaning (Kovacs and Lavigne, 1992). The lactation period of the hooded seal is the most extreme known lactation period of all mammals, lasting only 3 to 4 days (Bowen et al., 1985).

One hypothesis for this short lactation is that it reduces the maternal overhead (the total energy dedicated to maintain the maternal metabolism during the lactation period), hence maximizing the transfer of maternal energy stores to the pups (Fedak and Anderson, 1982). The relative cost of milk production is another selective pressure that appears to be influencing the length of lactation, since reduction of lactation period leads to reduction of milk energy output by the mother (Oftedal et al., 1987; Schulz and Bowen, 2005).
In addition, the proximity and richness of prey before the breeding season might be another possible explanation (Bowen et al., 1985; Costa, 1993). By an intense and short lactation, the probability of being preyed upon by polar bears (*Ursus maritimus*) before completion of energy transfer decreases (Costa, 1993). Furthermore, the unstable environment and increasing water distance between ice floes at the time the blue-backs are born might serve as a deterrent to polar bears, thus decreasing predation risk (Bowen et al., 1985; Schulz and Bowen, 2005).

The rate of energy transfer is exceptionally high during the lactation period. It was estimated that in hooded seals pups of the south east coast of Labrador, the rate of energy transfer was of 250 MJ per day, which is quite high compared to other mammals (Oftedal et al., 1993). This high energy transfer is facilitated by the high fat, low protein, sugar and water content of hooded seal milk. Milk composition also helps in blubber deposition in the pup.
During this nursing period, pups drink up to 10 kg of milk per day which allows them to gain on average 7 kg per day (Bowen et al., 1985; Oftedal et al., 1988; Oftedal et al., 1993). Aside from consuming large quantities of energy that far exceed the metabolic cost of the pups, this extraordinary daily weight gain is possible because of their high efficiency in converting the milk energy in new tissue. They achieve this by retaining at least 84% of the ingested energy and having a mass transfer efficiency of 63% (Oftedal et al., 1988; Kovacs and Lavigne, 1992; Oftedal et al., 1993).
Moreover, newborn hooded seal may reduce their metabolic cost since they are quite sedentary. They move only in order to approach the mother for nursing or when the mother and the pup are disturbed by male hooded seal adults (Lydersen and Kovacs, 1999).

At the end of the lactation period, pups are abruptly weaned when they are suddenly abandoned by the hooded seal mother. By this time, the newborn pups have doubled their birth weight (Bowen et al., 1985; Kovacs and Lavigne, 1992; Lydersen and Kovacs, 1999). After being weaned, hooded seal pups enter a post-weaning fast that approximately last four weeks, during which they lose 0.4 kg each day (Bowen et al., 1987).

Throughout this period, in the case of the pups of the West Ice, they passively follow the movement of the pack ice, while they learn how to swim, dive and capture food. It is not until roughly one month after being weaned, that pups leave the ice edge and become pelagic in the open sea waters of the North Atlantic until subsequent return to the ice after two and a half months (Bowen et al., 1987; Lydersen and Kovacs, 1999; Folkow et al., 2010).

1.2 Aims

Although, there has been some studies of the morphometrics of newborn hooded seals and the weaned seals, most of these studies were done on hooded seals belonging to the Northwest Atlantic stock (Bowen et al., 1985; Bowen et al., 1987; Kovacs and Lavigne, 1992; Oftedal et al., 1993), except for the study by Shepeleva (1973) which was done in hooded seals of the West Ice.

Nevertheless, in the last decades, the Greenland Sea population has seen a dramatic decrease of abundance, however, the causes behind the decrease are not completely understood. Could there be something happening during the lactation period that could be contributing to this decline in the population?

Thus, the aim of this thesis was to acquire more knowledge of the first days of life of these hooded seal pups. I examined the changes during the extreme lactation by inspecting the body composition of West Ice hooded seal pups at the beginning of the lactation period and at the end. Furthermore, the energy density of the different tissues was measured to estimate the extent of maternal investment (as energy deposition) before and after parturition. Energy deposition in newborns and weaned pups over the last 10 year, was estimated as well, in order to assess energetic changes that could be affecting pup survival.

2 Materials and Methods

Data from thirteen newborns and seventeen weaned seals was used in this thesis. These seals were captured in the West Ice in the Greenland Sea (approximate location 72°N and 15°W) during late March and early April from 2007 to 2018 (Table 1 & 2) as part of a bachelor/Master course (Bio- 2310) . The pups were captured on the ice floes using hoop nets and brought aboard the research vessel "Helmer Hanssen". Each expedition was granted permission by the Ministry of Fisheries and Hunting from the Government of Greenland and the Directorate of Fisheries from the Government of Norway for the capture of hooded seals for the collection of samples for scientific purposes.

Once on board, all animals were weighted using a Salter weight scale and identified. Pups were considered newborns based on the following criteria: fresh placenta, fresh blood on the ice and low body weight (< 35 kg). They were determined as weaned when the pups were found alone on the ice and had high body mass. Next, either on the same day of capture or the next day, the pups were killed by a lethal dose of pentobarbital (15-20 $mg \cdot kg^{-1}$) via the extradural-intravertebral vein or by a hakapik blow to the head (standard killing method).

2.1 Dissection

After death, all hooded seal pups followed similar dissection protocols. Seals from 2007 to 2018, were dissected on board of the research vessel after euthanasia. Before dissection, however, the weight of the buckets was noted first, in order to subtract it from the total weight of the tissue or organ that was to be measured. Measurements of body mass (BM) by means of a Salter scale weight, were taken after death.

Dissection started by first cutting the pups open through the skin and subsequent blubber layer along the median plane. Then, the depth of the blubber layer was recorded (not in all years). Flaying of the skin with blubber was done next. Afterwards, the blubber was carefully separated from the skin. The skin and the blubber were each put in different buckets, in order to weight them. Any blubber or fat remains on the core or within the internal organs was also collected and weighted together with the rest of the blubber. The core (internal organs, muscles and bones) was then weighted. Thereafter, the internal organs were located and identified. The lungs, the heart, the intestines, the stomach, the liver, the kidneys, the spleen and the digestive system were weighted separately. The digestive system consisted of the intestines, oesophagus and stomach. Next, the different muscle groups were dissected off the skeleton, gathered into a bucket, and their mass measured. The total bone mass was weighted as well. However, previous to the weight measurement of the total bone mass, the brain and eyes were removed from the skull.

The two weaned seals that were captured in April 2017, underwent a similar protocol to the previous seals. However, they were not dissected immediately after death. After death, they were wrapped in plastic bags and stored in a freezer at -20ºC until the arrival at Tromsø. In Tromsø, the animals were kept at -20ºC for approximately four months. Before dissection, they were left to thaw from 28.08.17 till 31.08.17 (S.28) and from 4.09.17 till 7.09.17 (S.29) at an average of 10ºC. The dissection was done in the same manner as the previous seals.

2.2 Sample collection

After weighting the blubber/fat, the organs and the muscles of each of the two seals (S.28 & 29), some samples were collected. In order to homogenize the internal organs of each seal, the internal organs were cut into pieces and mixed together using a commercial blender. The blubber/fat and muscles were treated likewise. After blending, samples of 45-50 ml were taken of the mixture of internal organs, blubber/fat muscles and stored in sterile centrifuge tubes in the freezer at -20ºC, to prevent decomposition, until further treatment of the samples. In total, eleven samples were taken from each seal, three of a mixture of the internal organs, four of blubber and four of muscles.

2.2.1 Drying

In October 23th, 2017, the samples of S.28 were taken out and left to thaw overnight in a refrigerator (4-5ºC). The next day, the samples were taken out. Of each sample, 20 ml were put in plastic beakers and were covered with parafilm. With the use of a needle, holes were made on the parafilm, to allow the water vapor to leave. The samples were then put to dry in an oven (TS4057, Termaks, Bergen, Norway) at 60ºC, for a minimum of 50 hours. A bowl of silica gel was put together with the samples, to prevent reabsorption of water vapor. Water loss of the samples was monitored through their weight. Nine measurements were taken, one before they were put to dry and eight during the drying period. The samples were taken out until they weight loss was no longer significant (Fig.1). Samples of seal 29 followed the same procedure (Fig.2).

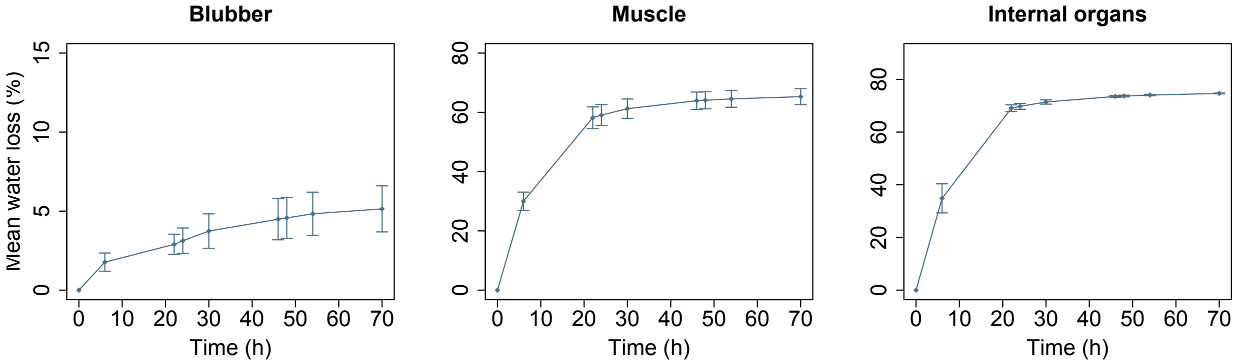

Fig. 1. Shows the average percentage of water loss (± SD) over 70 hours of blubber, muscles and internal organs of S.28.

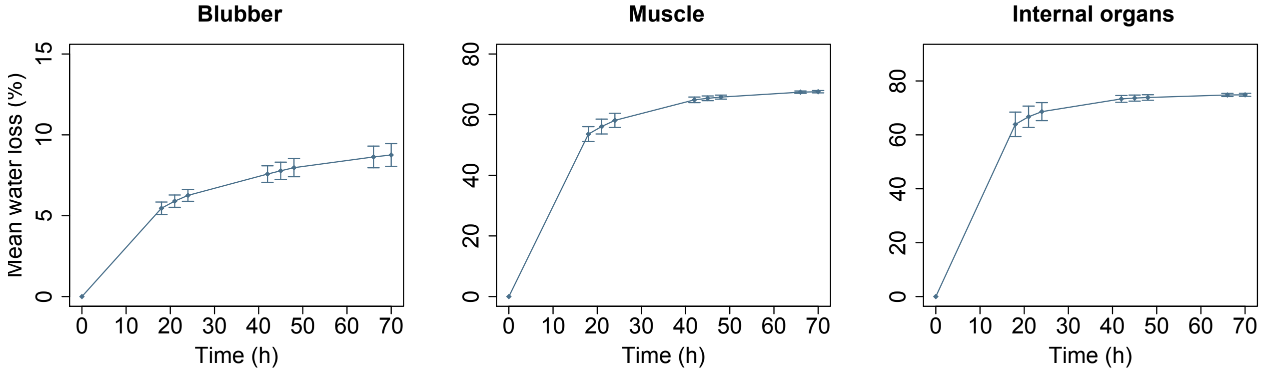

Fig. 2. Shows the average percentage of water loss (± SD) over 70 hours of blubber, muscles and internal organs of S.29.

Samples were left to cool for four to five hours in a glass vacuum desiccator (200 mm diameter) together with the desiccant. Subsequently, blubber samples were transferred to 20 ml polyethylene vials. Muscles and internal organ samples were grinded in an analytical mill (A10, IKA, Germany) and then transferred to 20 ml polyethylene vials as well. Then, the samples were frozen (–20 ºC) until transportation for further analysis.

2.3 Transportation and analysis of samples

Prior transportation, the frozen samples were securely packed. Samples were sent to the Norwegian University of Life Sciences, where their energy density was analyzed by bomb calorimetry (1281, PARR)

2.3.1 Bomb calorimetry

A bomb calorimeter is used to measure the transferable energy of biological materials by measuring the heat increase that occurs when a sample is burned.
At the Norwegian University of Life Sciences, it is used primarily for the determination of energy in poultry feed, intestines and fertilizer samples, as well as other organic materials and liquids.

The combustion of the sample is done in a system that cannot exchange heat with the outside environment (closed system). The sample is placed on a crucible, which it is fixed on the lid of the bomb. Later, it is filled with excess oxygen, pressurizing the bomb at typically 30 atm. Next, the bomb is placed in a calorimeter vessel with known water weight. A current, then, ignites the sample, which releases heat by combustion. During combustion, the organic molecules will be converted mainly to CO_2 and H_2O (Equation 1).

Equation 1. $CH_4 + 2O_2 = CO_2 + 2H_2O$

This heat flow increases the temperature of the steel bomb and its contents. The surrounding water jacket´s temperature is increased as well by the activation of the bridge circuit (ensures the same temperature in the water jacket as in the calorimeter vessel). Temperature change, then, is measured by a thermometer. Together with the bomb factor, it is used to calculate the amount of energy that is released by the combustion of the sample (McLean and Tobin, 1987).

2.4 Calculations

Blood loss was calculated by subtracting the blubber/fat and skin and core mass from the total mass (Equation 2).

Equation 2.

$$Estimated\ blood\ loss\ [kg] = Total\ mass\ [kg] - (Total\ blubber\ [kg] + core\ mass\ [kg] + Skin\ [kg])$$

Body composition was estimated by calculating the relative mass of each organ and tissue (Equation 3) to the total body mass (BM).

Equation 3.

$$Relative\ mass_{\mathrm{Organ/Tissue}}\,[\%] = \frac{Mass_{Organ/Tissue}\ [\mathrm{kg}]}{Total\ Mass\ [\mathrm{kg}]} \times 100$$

Energy content stored in the blubber/fat, internal organs and muscles was estimated using Equation 4. and the respective energy equivalent. Energy content was estimated to be 38.2 (SEM ± 0.08), 21.4 (SEM ± 0.14), 24 (SEM ± 0.3) MJ/kg, for blubber, internal organs and muscles respectively. Skin and skeleton were assumed to not contribute energy; hence their energy content was not calculated. Body composition was also estimated in terms of energy, for which Equation 5. was used.

Equation 4.

$$Energy\ content\ \lfloor MJ \rfloor = Mass_{Organs/Tissue}\ \lfloor kg \rfloor \times Energy\ equivalent\ \left\lfloor \frac{MJ}{Kg} \right\rfloor$$

Equation 5.

$$Relative\ energy_{\mathrm{Organ/Tissue}} \lfloor \% \rfloor = \frac{Energy_{Organ/Tissue}\ \lfloor \mathrm{MJ} \rfloor}{Total\ Energy\ \lfloor \mathrm{MJ} \rfloor} \times 100$$

Basal metabolic rate (BMR) of the seals was estimated by using the Kleiber´s equation (Equation 6). Immature pinnipeds, however, have metabolic rates that are two times higher than the values predicted by the Kleiber´s equation (Lavigne et al., 1986). Therefore, the field metabolic rate (FMR) of the newborn and weaned seals was calculated by Equation 7.

Equation 6.

$$BMR\ \left\lfloor \frac{kcal}{day} \right\rfloor = 70\ \ BM \lfloor kg \rfloor^{0.75}$$

Equation 7.

$$FMR\ \left\lfloor \frac{kcal}{day} \right\rfloor = 2 \times BMR$$

For the determination of the capacity to fast, it was assumed that only 50% of the proteins and 70% of the blubber/fat are possible to mobilized in practice. Energy available from blubber and proteins, was estimated using Equations 8 & 9, respectively. The total available energy (AE) was then converted to kcal (1 MJ= 239 kcal) and divided by the FMR, in order to estimate a theoretical fasting capacity during the post weaning fast (Equation 10).

Equation 8.

$$Energy\ content_{Fat}\lfloor MJ\rfloor = Mass\ \lfloor kg\rfloor \times\ Energy\ Equivalent\ \times\ 0.7$$

Equation 9.

$$Energy\ content_{Proteins}\lfloor MJ\rfloor = Mass\ \lfloor kg\rfloor \times\ Energy\ equivalent\ \times\ 0.5$$

Equation 10.

$$Fasting\ capacity\ \lfloor days\rfloor = \frac{AE\ \lfloor kcal\rfloor}{FMR\ \left\lfloor \frac{kcal}{day}\right\rfloor}$$

In addition, the energy deposited on average (ED) in the pups during the lactation period can be estimated by subtracting the total energy on average of the newborn seals (TEN) from the total energy of the weaned seals (TEW) (Equation 11).

Equation 11.

$$ED = TEW - TEN$$

Lastly, maternal energy investment (MEI) was measured as energy deposition in the pups. However, for comparison it is expressed relative to maternal size (Equation 12) (Oftedal et al., 1993).

Equation 12.

$$MEI\left[\frac{MJ}{kg}\right]=\frac{Energy\ deposition_{Stage}\ [MJ]}{Maternal\ mass\ [kg]}$$

2.5 Statistics

Bones, muscles and heart mass comparisons between the two stages were done using unpaired two-samples t-test, while body mass, blubber mass and internal organs mass were compared using Welch two Sample t-test. Blood, skin, lung, digestive system, liver, kidney and spleen weight were compared using Mann-Whitney-Wilcoxon test since the data had no normal distribution (Shapiro Wilk test). Theoretical fasting capacity was compared using unpaired two-samples t-test. The amount of energy deposited during pregnancy and during the lactation period over the last 10 years was tested using a simple linear regression. Significant statistical difference was indicated by $P < 0.05$. Values are given as means ± standard error of the mean (SEM).

3 Results

Table 1. Shows the sex, date of capture, location of capture and weight of newborn seals.

X- no data available

*Data collected by students of the Arctic biology course (Bio-2310) from 2007-2018. All seals were captured in the area 71 ºN/ 19 ºW and 72 ºN/ 15 ºW

Seals	Capture date	Sex	Weight (kg)
S.1	24-26/03/2007	Male	23.0
S.2	25/03/2010	Unidentified	24.5
S.3	26/03/2010	Unidentified	24.5
S.4	31/03/2011	Male	30.5
S.5	26/03-1/04/2011	Unidentified	29.5
S.6	19-30/03/2013	Unidentified	26.7
S.7	19-30/03/2013	Male	31.0
S.8	24/03/2014	Male	24.0
S.9	25/03/2014	Male	25.2
S.10	23/03/2015	Male	26.2
S.11	23/03/2015	Female	25.0
S.12	22-26/03/2016	Male	20.5
S.13	22-26/03/2016	Male	19.0
S.14	28/03/2018	Female	21.2

Table 2. Shows the sex, date of capture, location of capture and weight of weaned seals.

X- no data available

*Data collected by students of the Arctic biology course from 2007-2016. All seals were captured in the area 71 ºN/ 19 ºW and 72 ºN/ 15 ºW

Seals	Capture date	Sex	Weight (kg)
S.15	24-26/03/2007	Male	45.0
S.16	25/03/2010	Unidentified	38.5
S.17	25/03/2010	Unidentified	62.5
S.18	27/03/2011	Male	44.0
S.19	26/03-1/04/2011	Female	48.0
S.20	19-30/03/2013	Unidentified	49.8

Seals	Capture date	Sex	Weight (kg)
S.21	27/03/2013	Unidentified	47.5
S.22	23/03-1/04/2014	Male	36.0
S.23	23/03-1/04/2014	Male	44.1
S.24	23/03/2015	Female	56.5
S.25	20-27/03/2015	Male	56.4
S.26	21/03/2016	Female	37.0
S.27	22-26/03/2016	Female	31.7
S.28	09/04/2017	Female	46.5
S.29	09/04/2017	Female	37.8
S.30	28/03/2018	Female	45.0
S.31	25/03/2018	Male	39.0

3.1 Body composition

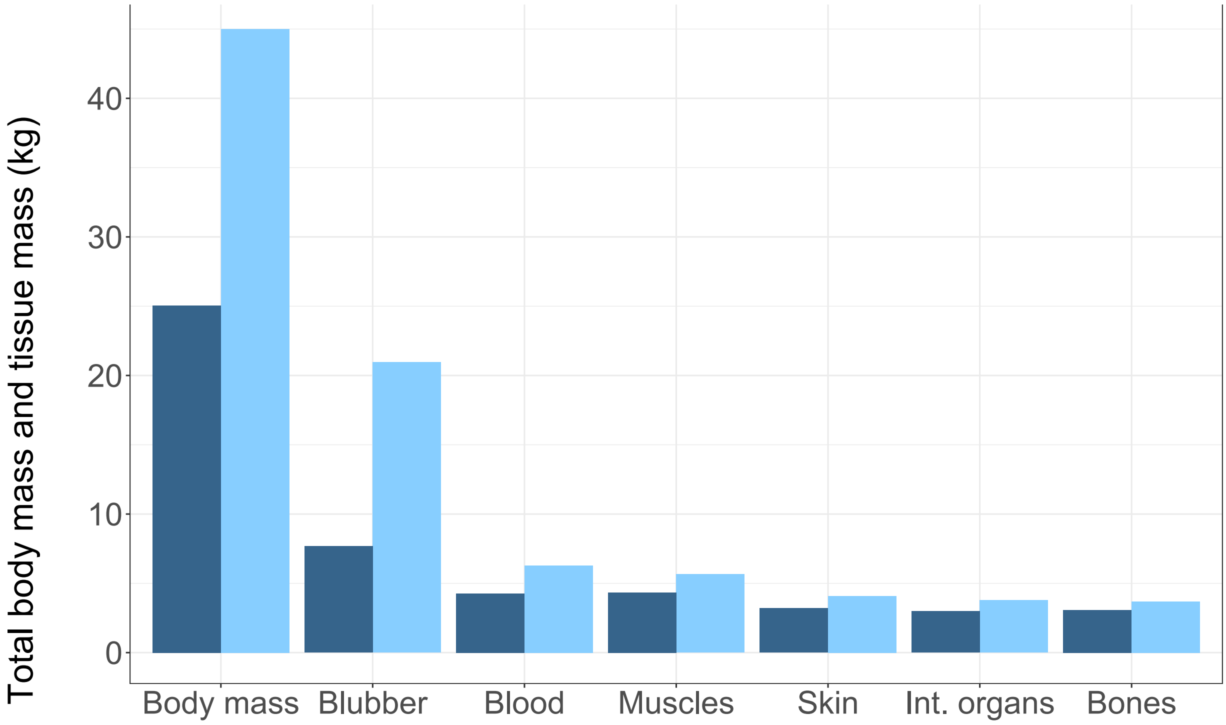

Fig. 3. Body, blubber, muscle, bone, skin and internal organ mass (kg) in newborn (dark blue) and weaned pups (light blue).

On average the body mass of newborn seals was 25.1 ±1 kg, which was significantly different compared to 45.0 ± 2 kg, the average body mass of weaned seals (P < 0.0001).

The main body component of newborn seals and weaned seals, was blubber. Blubber in newborns compromised 30,7 ± 2.9 % and in weaned pups 46.6 ± 1.7 %, (Fig.4). Blubber/fat mass was significantly different (P < 0.001) between newborns and weaned pups, where newborns had deposited 7.7 ± 0.8 kg, while by the end of lactation pups had deposited 21.0 ± 1.2 kg of blubber (Fig.3).

Total muscles mass in newborn blue-backs was 4.3 ±0.2 kg, which represented 17.3 ± 0.6 % of the total mass. In weaned seals, on the other hand, muscle mass increased to 5.6 ± 0.3 kg, however at this developmental stage it represented only 12.7 ±0.6 % (Fig.3 &4) of the body mass.

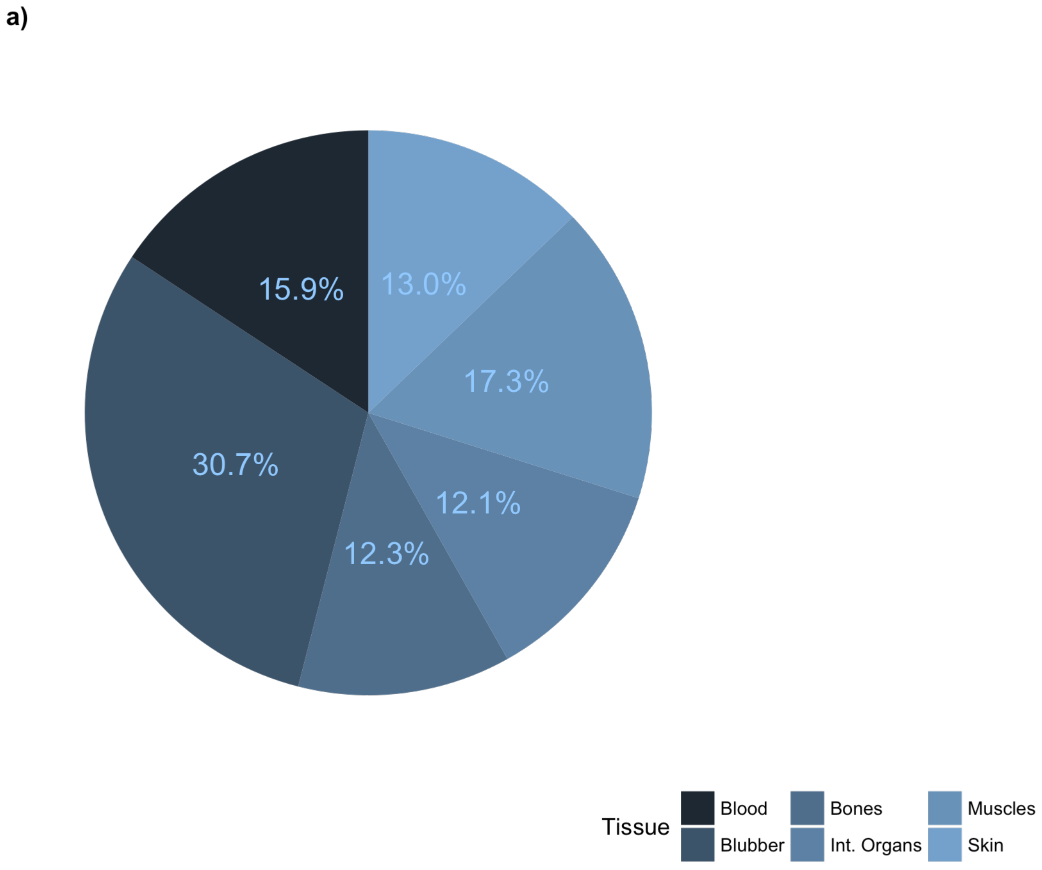

Fig. 4. Shows body composition as percentage of total body mass for a) newborns and b) weaned seals.

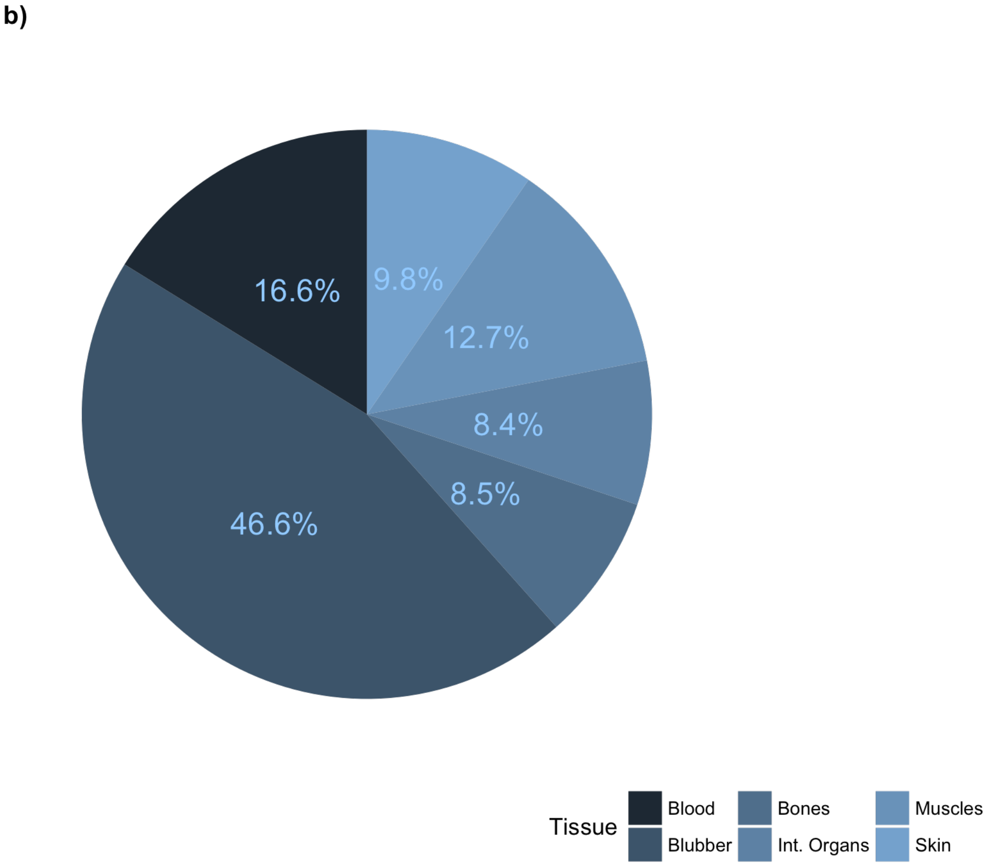

Fig. 4. Shows body composition as percentage of total body mass for a) newborns and b) weaned seals.

Bone mass in newborns, weighted, 3.1 ± 0.1 kg, while mean viscera weight was 3.0 ± 0.1 kg. Median skin weight was 3.2 kg (0.8 to 4 kg). Weaned seals had 3.7 ± 0.2 kg of bones mass and 3.8 ± 0.2 kg of internal organs mass. Skin mass median weight was 4.1 (2.9 to 6.4 kg). Internal organs, skin and bone proportions decreased, so that at weaning, they represented 8.4 ± 0.4 %, 9.8% (7.1 to 12.9 %) and 8.5 ± 0.5 % (Fig. 4b), respectively.

The median blood weight was not statistically different in weaned (6.1 kg, range 2 to 21.8 kg) and newborn seals (4.2 kg, range 0.6 to 6.9 kg) ($P > 0.05$) (Fig.3). In newborns blood weight corresponded to 15.9 ± 1.8 % (Fig.4a) of the total mass, whereas in weaned seals it was calculated to be 16.6 ± 2.3 % (Fig.4b).

3.1.1 Mass increase during lactation

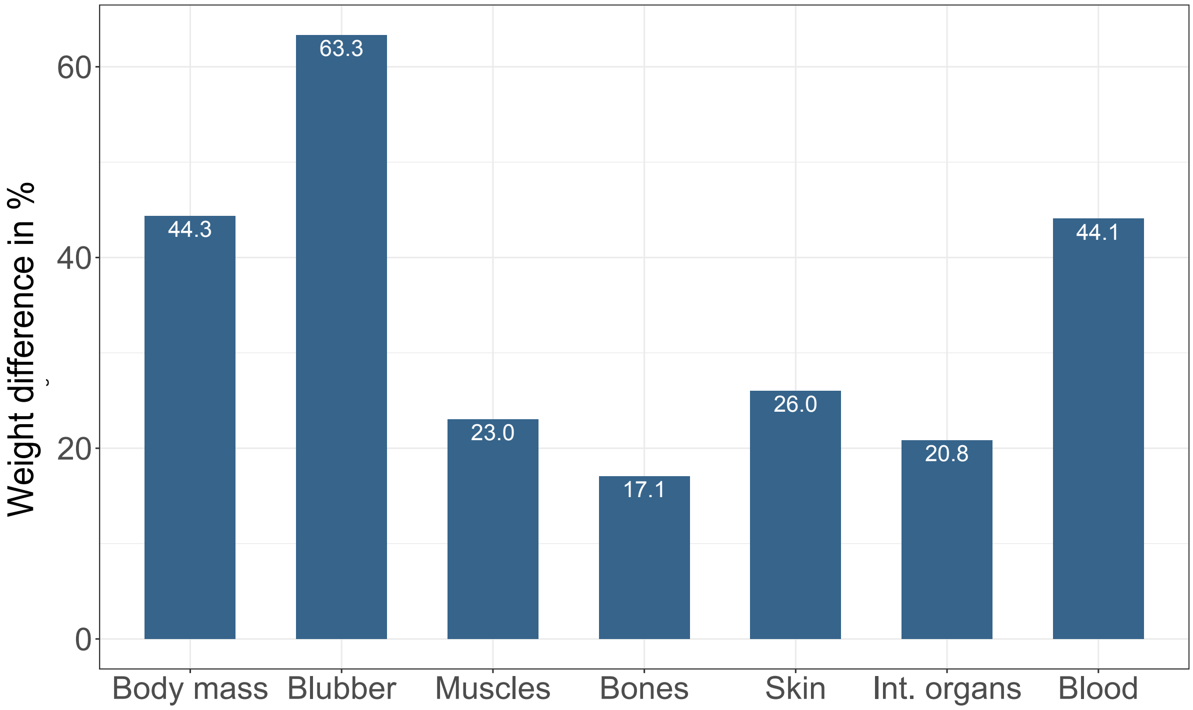

Fig. 5. Shows the weight increase during the lactation period as percentage of body mass, blubber, bones, internal organs, muscle and skin.

During the lactation period the mass all tissues significantly increased ($P < 0.05$), except for blood, which did not change significantly ($P > 0.05$). Body mass increased 44 % by the end of the nursing period. Assuming that the pups suckle for 4 days (Bowen et al., 1985) and that they gained on average 20 kg at the end of the lactation period, then pups would gain roughly 5 kg/day . Blubber/fat mass increased 63 %, followed by the significant increase in skin weight (26 %). Muscle mass and mass of internal organs increased 23 % and 21% during this period (Fig.5). Whereas bone mass showed the lowest increase (17 %).

3.2 Energy content

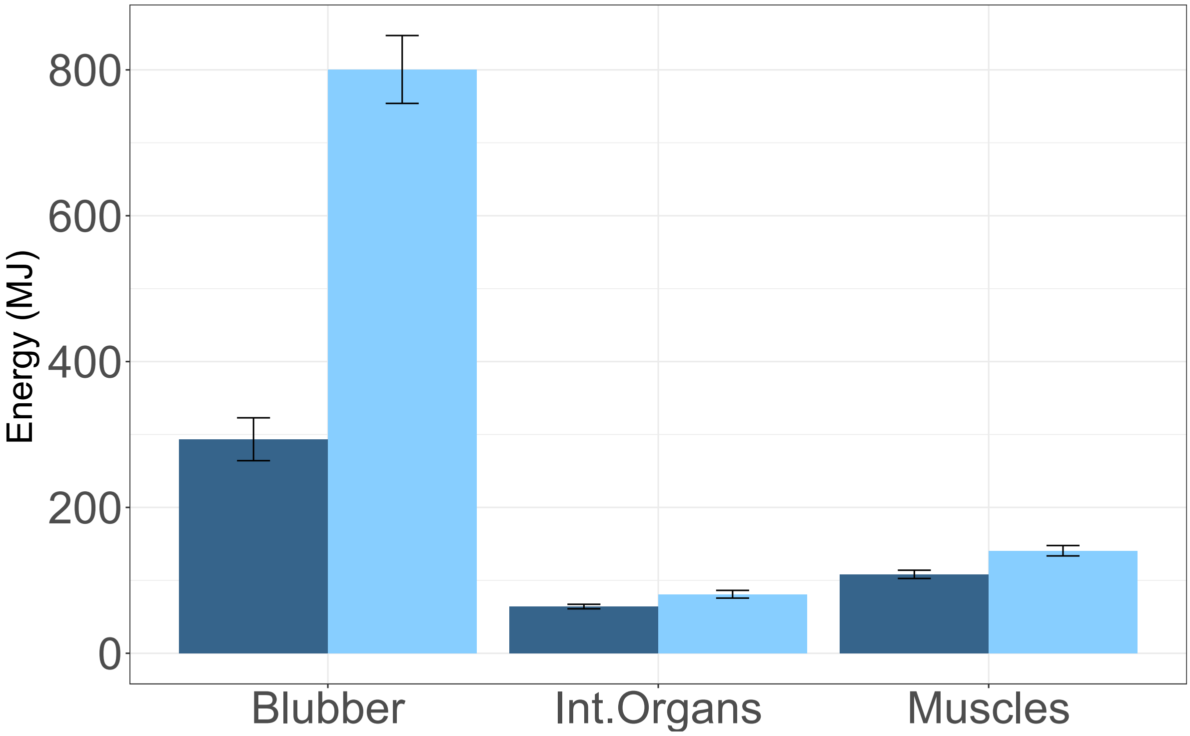

Fig. 6. Total blubber, muscle and internal organs energy density (MJ) ± SEM in newborns (dark blue) and weaned pups (light blue).

Total average energy content of blubber, muscles and internal organs, increased significantly ($P < 0.05$) during lactation. Total blubber energy content in newborns was 293.5 ± 29.4 MJ, while in weaned pups it had increased to an average of 800.6 ± 46.5 MJ. The total energy energy content in muscles was 108.2 ± 5.7 MJ and 140.6 ± 7.1 MJ, for newborns and weaned seals, respectively.

Compared to the average energy stored in muscle and fat, energy content of the internal organs was lower. In newborns, mean energy storage was 66.0 ± 2.6 MJ and weaned seals had significant higher energy stores of 83.0 ± 5.8 MJ (Fig.6) ($P <0.05$). In total, blubber stored 60 ± 2.3 % of the total energy in newborns, while in weaned seals it constituted 78 ± 1% (Table 3).

Table 3. Relative amount of energy of all blubber and muscle (proteins) in newborn and weaned seals expressed in percentage.

	Newborns (*n* = 14)		**Weaned pups** (*n* =17)		**P**
	Mean	Sem	Mean	Sem	
Blubber (%)	61.4	2.6	78.0	1.0	< 0.05
Proteins (%)	38.5	2.6	22.0	1.0	< 0.05

3.2.1 Energy increase

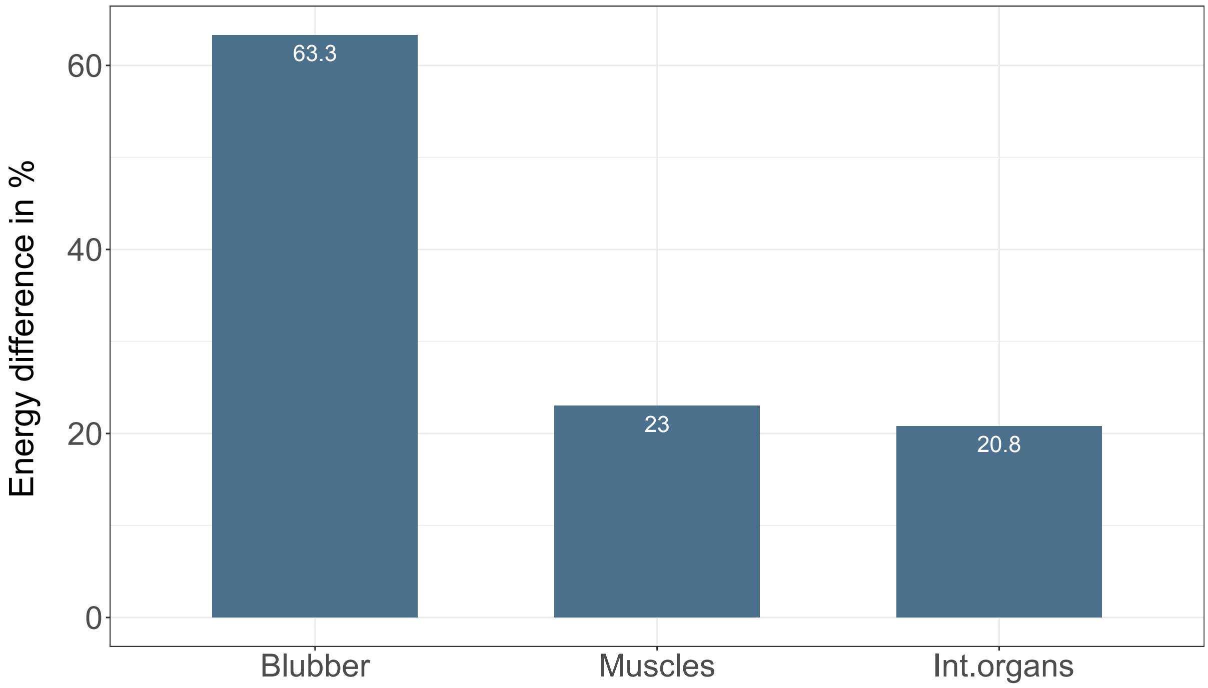

Fig. 7. Percentage of energy increase during the lactation period in blubber, muscles and internal organs

As mass increased during this period, the amount of energy stored in each tissue and organs significantly increased as well ($P < 0.05$). Blubber/fat energy content increased by 63%. On the other hand, the energy content of muscles and internal organs increased by 23% and 21 % respectively (Fig. 7).

3.3 Theoretical fasting capacity

Table 4. Estimated field metabolic rate(FMR), mobilizable energy and fasting capacity (days) of newborn seals.

Newborn	FMR	Mobilizable kcal	Days
Seal 1	1500	75200	51
Seal 2	1500	51500	33
Seal 3	1500	70600	46
Seal 4	1800	111000	61
Seal 5	1800	758000	43
Seal 6	1600	61200	37
Seal 7	1800	69200	38
Seal 8	1500	61900	41
Seal 9	1600	64900	41
Seal 10	1600	86900	54
Seal 11	1600	63500	41
Seal 12	1300	50900	38
Seal 13	1300	43200	34
Seal 14	1400	90000	65
Mean	1600	69700	44
SD	170	17600	10
SEM	45	4710	3

Table 5. Estimated field metabolic rate (FMR). mobilizable energy and fasting capacity (days) of weaned pups.

Weaned	FMR	Mobilizable kcal	Days
Seal 15	2400	171000	70
Seal 16	2200	176000	81
Seal 17	3100	273000	88
Seal 18	2400	191000	80
Seal 19	2500	225000	88
Seal 20	2600	207000	79
Seal 21	2500	204000	80
Seal 22	2100	123000	60
Seal 23	2400	154000	64
Seal 24	2900	153000	53
Seal 25	2900	221000	77
Seal 26	2100	160000	76
Seal 27	1900	121000	64

Weaned	**FMR**	**Mobilizable kcal**	**Days**
Seal 28	2500	156000	63
Seal 29	2100	159000	74
Seal 30	2400	191000	79
Seal 31	2200	147000	67
Mean	2400	178000	73
SD	330	39200	10
SEM	80	9500	2

The fasting capacity of newborns was calculated to be 44 ± 3 days on average, when relying only on their energetic stores. Weaned seals, however, had a theoretical fasting capacity of 73 ± 2 days, which was statistically different than the newborn seal fasting capacity ($P < 0.05$).

3.4 Maternal investment strategies

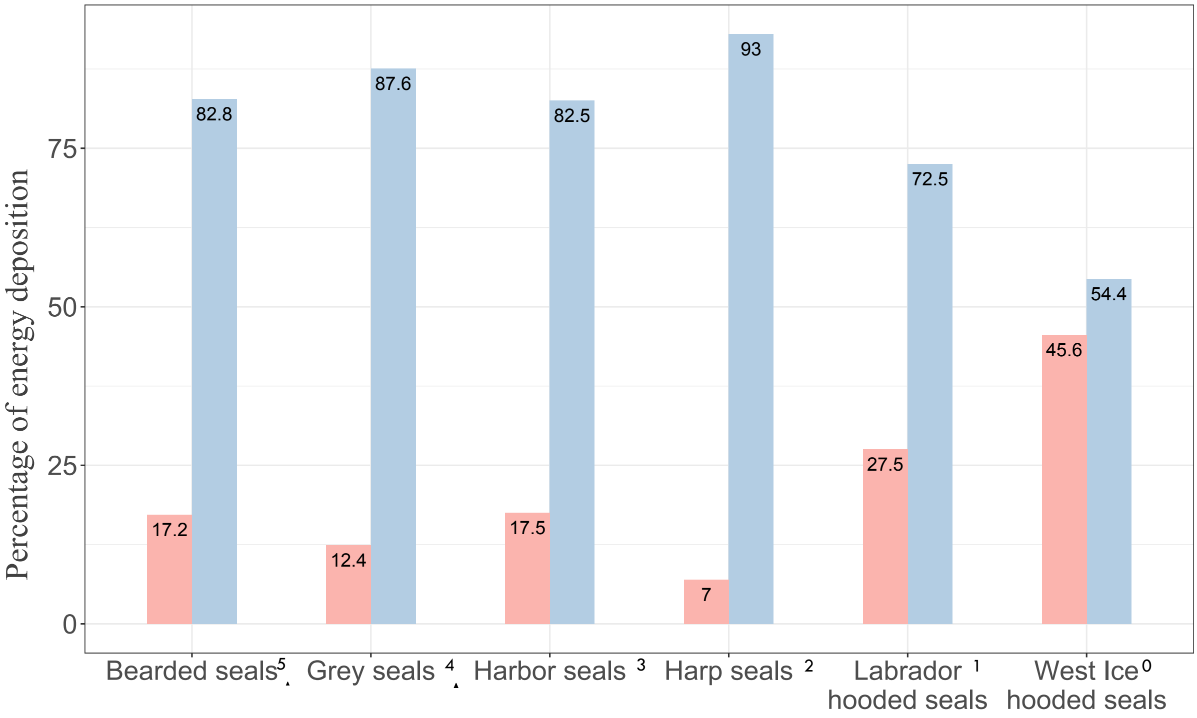

Fig. 8. Shows the percentage of energy deposition in bearded, grey, harbor, harp, Labrador hooded seal and west ice hooded seal, in newborn pups(pink) and during lactation (blue). Data from: 0. This study. 1. Oftedal et al. (1993). 2. Oftedal et al. (1996). 3. Bowen et al. (1992). 4. Iverson et al. (1993). 5.Lydersen and Kovacs (1999) and Lydersen et al. (1996).

West Ice hooded seals appear to have a different energy deposition strategy than the Labrador hooded seals, as well as other members of the phocid family. Bearded seals, grey seals (*Halichoerus grypus),* harbor seals (*Phoca vitulina)* and harp seals (*Pagophilus groenlandicus*) deposited 80-93% of the total energy at weaning during the lactation period, which is different from both populations of hooded seals. Labrador female hooded seals deposited roughly 28% of the total energy of a pup at weaning during the lactation period, while West Ice hooded seals deposited approximately 46% (Fig 8.).

The mean energy deposition in newborns of the West ice population was 18.6 MJ/kg which is significantly greater ($P < 0.001$) than in newborn hooded seals of the Southern eastern

Labrador stock. Furthermore, weaned pups had, as well an average energy deposition that was statistical different for both subpopulations ($P < 0.05$) (Table 6).

Table 6. Energy deposition (MJ/kg) in newborn (*n* = 14) and weaned pups (*n*= 17) of the West Ice and newborns (*n*= 4) and weaned pups (*n*= 5) of off Labrador Sea.

	West Ice Hooded seals		**Labrador Hooded seals**[1]		**P**
	Mean	Sem	Mean	Sem	
Newborns (MJ/kg)	18.6	0.95	10.1	0.25	<0.0001
Weaned (MJ/kg)	22.8	0.65	20.2	0.79	0.03

1. Data from: Oftedal, et al. 1993. Energy Transfer by Lactating Hooded Seals and Nutrient Deposition in their Pups during the Four Days from Birth to Weaning.

3.5 Energy deposition during pregnancy and lactation: time series 2007-2018

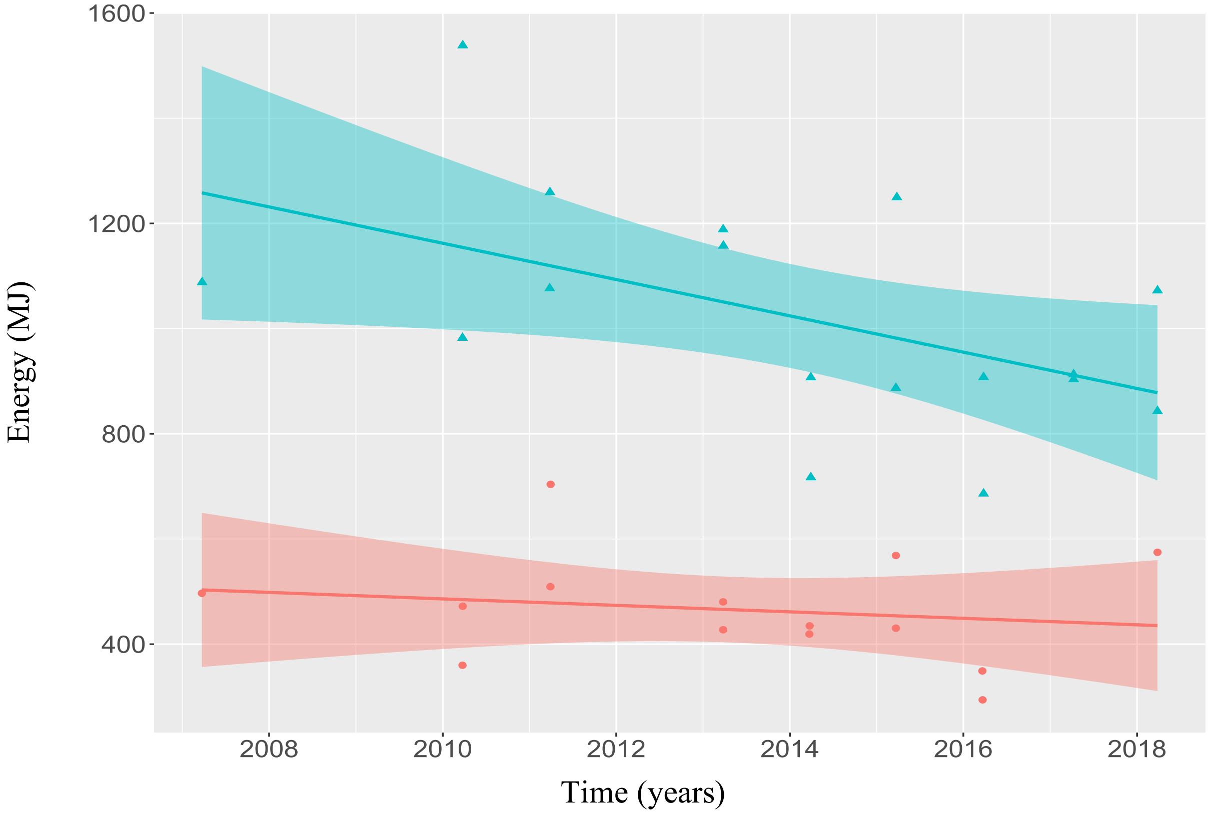

Fig. 9. Shows energy deposition (MJ) as a function of time (years) for newborns (red dots) and weaned seals (aqua triangles). A linear regression based on the average of the two seals in each year (except for the year 2007) is included. It shows a significant relation ($P < 0.05$) between the two parameters ($R^2 = 0.21$). 95% confidence interval is given for the newborn pups (red shaded area) and for the weaned pups (green shaded area).

Energy deposition during the last ten years, shows a significant negative trend in weaned hooded seals ($P < 0.05$). The data suggests that there has been a 30% decrease in energy deposition of pups at weaning. Newborn seals, however, during the same period of time, do not show a decrease in energy deposition.

4 Discussion

Phocid seals are distinguished for their short lactation period that can last from 3-4 days to 2 months. Hooded seals take this reproductive strategy to the extreme, by devoting only 4 days to the nursing of their pups (Bowen et al., 1985; Oftedal et al., 1987; Bowen, 1991).

Throughout this brief lactation period, hooded seals pups have to gain enough weight and energy for the sake of their survival. In a study done by Shepeleva (1973), it was found that the mass of newborn hooded seals ranged from 23 to 30 kg in the West Ice population. However, the study was poorly documented since the criteria for determining pup age was ungiven. Unexpectedly, the mass range described by Shepeleva (1973) was quite similar to the results of the present study (19 -31 kg) (Table 1).
Since then, mass at birth of hooded seal pups has been reported in more detailed studies, but only for hooded seals of the Northwest Atlantic population (Bowen et al., 1985; Bowen et al., 1987; Kovacs and Lavigne, 1992; Oftedal et al., 1993). The mean birth weight observed for southern eastern Labrador newborns was of 22.0 ± 0.61 kg ($n = 21$) (Bowen et al., 1985) and 23.7 ± 2.6 kg ($n = 4$) (Oftedal et al., 1993) and for the study on northeastern off Newfoundland newborn, it was 21.5 ± 0.9 ($n = 13$) kg (Bowen et al., 1987). Compared to these, the values presented by Kovacs and Lavigne (1992) for hooded seals off the Gulf of St. Lawrence (24.5 ± 2.6 kg, ($n = 19$)) and the values found in this study, where the average newborn weight was of 25.1 ± 1.0 kg ($n = 14$) (Fig.3), differ only slightly.

At weaning, mean body mass was almost double the birth mass (45.0 ± 2 kg, $n = 17$) (Fig.3). The average body mass at weaning in this study was similar to the mean body mass documented for the newborns of southern eastern Labrador and northeastern off Newfoundland, which were 42.6 ± 1.37 kg ($n = 11$), 43.2 ± 1.6 kg ($n = 12$) and 43.7 ±1.9 kg ($n = 5$), respectively. Mass at weaning for the Gulf of St. Lawrence pups was higher than in the other locations, with an average of 47.1 ± 6.7 kg ($n = 25$). However, it equally produces the largest variation, suggesting that it is very different to the other mean weaning masses.

The differences between the weaning masses may reflect possible mass differences of female hooded seals at parturition of the diverse areas, since it appears that larger females are able to wean larger pups (Kovacs and Lavigne, 1992) .

4.1 Body composition

4.1.1 Newborn seals

The most important proportion in the body of a newborn hooded seal pup was fat (31 %) (Fig.4a). The amount of body fat (7.7 ± 0.8 kg) for newborn pups in this study was more than the double compared to the results found in hooded seals of the Gulf of St. Lawrence (14%) (Kovacs and Lavigne, 1992).
The difference on fat proportion of newborns could be a result of erroneously determining a mid-lactation pup as a newborn pup, since their suckling period is so short, just a few hours after birth could biased the results.
Moreover, the data in this study was collected by different students each year, which could have introduced experimental errors due to variability in methodologies.
Although, the sample size of both studies is small and the fact that they were carried out in different decades, the variation in percentage of body fat may also be a reflection of the different maternal strategies of hooded seals on the West Ice and those on the Gulf of St. Lawrence.

Regardless, the fact remains that newborns have a high proportion of fat, compared to other phocid seals and other newborn mammals which are relatively low on body fat (Spray and Widdowson, 1950; Widdowson, 1950; Kuzawa, 1998). For example, harp seals, which are born in the same environment as hooded seals, are born with only 6% ($n = 3$) of fat (Worthy and Lavigne, 1983).

Such a high proportion was to be expected considering the extremely short lactation period of this species. Having this brief lactation means that energy and mass transfer from mother to pup will be restricted by time. Thus, being born with quite a high prenatal investment is an advantage for this species.

Fat is mostly deposited as a thin blubber layer. However, not only does this blubber layer helps reduce postnatal transfer but it is also involved in thermoregulation since it serves as a form of insulation against the cold environment (Bowen et al., 1987; Liwanag et al., 2012). Furthermore, the blubber layer may also help provide buoyancy (Liwanag et al., 2012).

By being born with this subcutaneous blubber layer, they can go into the water earlier than other phocids without suffering the risk of hypothermia. Therefore, this form of insulation, may be more advantageous for the hooded seal pups than the lanugo that most phocids are born with due to their short lactation period and environmental conditions that facilitates early immersion in arctic waters. (Bowen et al., 1987; Oftedal et al., 1991; Lydersen and Kovacs, 1999). Moreover, a higher fat content at birth may allow hooded seal pups to fatten more easily. It has been documented that lipoprotein lipase activity increases with increasing body fat, which means a higher lipid uptake and also facilitates blubber deposition (Iverson et al., 1995; Mellish et al., 1999).

The high blubber proportion means that the remaining body components will have a lower proportion than if the quantity of blubber was smaller, as what happens in other seals. The proportions of the viscera (12 %) and skin (13 %) in the newborn pups (Fig. 4b) are much smaller compared to skin (17 %) and viscera percentage (20 %) found in harp seal newborns (*n* = 3), with a lower fat proportion (Lydersen and Kovacs, 1999).

4.1.2 During lactation

During the lactation period, the transfer of mass between mothers and pups is quite intense. In only 3 to 4 days that the lactation period lasts, mothers have to ensure that appropriate quantities nutrients are transferred to the pup to guarantee a normal development and survival for the pup.

In previous studies, for a different population of hooded seals, the mean rate of mass gain of the species was determined to be 7 kg per day (Bowen et al., 1985). In the present study, the mass gain per day was estimated to be 5 kg/day, lower than the value given by Bowen et al.

(1985) but similar to the value documented by Oftedal et al. (1993). Nevertheless, recently weaned pups, could have been fasting for a couple of days when they were captured, underestimating mass at weaning. In this way, the total mass gained during weaning could be lower than the real value.

During this suckling period, hooded seals pups have been observed to not consume water or snow, just maternal milk. The estimated milk consumed for a 7 kg/day of mass gain rate, was 10.2 kg (Oftedal et al., 1993). If it is assumed that the rate of milk consumption is the same for both populations and that the average daily weight gain is 5 kg for the West Ice population, then pups would drink on average 7 kg of milk each day. Could this lower milk consumption, and thus lower mass gain rate, be the result of the greater head start that hooded seals newborns of the West Ice appear to have?

The transfer of nutrients from mothers to pups in hooded seals is more efficient than in most phocids, which supports the hypothesis that abbreviation of lactation leads to a reduction of maternal overhead cost and allows efficient nutrient transfer (Bowen et al., 1987; Oftedal et al., 1993).

4.1.3 Body composition of weaned pups

Over the course of the nursing period, pups increased their weight by 44 % (Fig.5). Weight gained was predominantly blubber (70%), so that at the end, at weaning pups had a blubber mass of 21 ± 1.2 kg (Fig.3). Moreover, pups can gain more energy through fattening than when they gain in lean body mass (Blaxter, 1989).Thus, this blubber mass increase is to be expected in a species where energy and mass efficiency is critical for the survival of the species.

Rapid blubber deposition is facilitated by the hooded seal milk composition, which is composed mainly of fat (61%) (Oftedal et al., 1988). Hooded seal pups are so efficient at blubber deposition, that they can absorb approximately 88 % of the ingested fat (Oftedal et al., 1993).

Apart from blubber, there is also significant increase of muscle mass (23%) and skin mass (26%) (Fig. 5) throughout the nursing period. Mass increase of skin is probably caused by the growth of the pup, since during nursing there is not only fattening happening but the pup also increases in length (Bowen et al., 1987). The same can be said about muscle mass increase. At birth, pups will have underdeveloped muscles. However, during the course of the nursing period, newborns spend most of their time either suckling or sleeping (Bowen, 1991; Perry and Stenson, 1992; Lydersen and Kovacs, 1999). Therefore, muscles involved in neck movement, crucial for suckling will be developed, as well as for locomotion on land, in contrast to those used for aquatic locomotion which will be hardly developed during this stage (Lestyk et al., 2009).

Bone mass changed significantly during the lactation period from the 3.1 ± 0.1 kg at birth to 3.7 ± 0.2 kg at weaning. During the nursing period, the increase of bone mass (17 %) was the lowest for all body compartments (Fig. 5). Moreover, in a previous study, length increased only 7% (Bowen et al., 1987). This suggests that skeletal growth is slow during this period. Nevertheless, slow skeletal growth during the lactation period can be observed in other pochid species as well, for example the harp seal and harbor seal (Kovacs and Lavigne, 1985; Cottrell et al., 2002).

4.2 Energy stores

4.2.1 Newborn seals

As observed before, hooded seal pups will fast after weaning for approximately a month. Thus, energy storage in these pups is quite vital. This is the reason why blubber has such significance. The energy density of blubber as stored in the body is 8 times higher than stored carbohydrates and proteins, thus it allows for the majority of the stored energy to be located on the thin blubber layer when they are born (61 %) (Table 3). There are some variations, however, when comparing the quantity stored in the blubber of newborn hooded seals of both populations, the Northwest Atlantic stock and Northeast Atlantic stock. In a previous study by Oftedal et al. (1993), it was determined that in newborns 54 % of the total energy was stored in the adipose tissue, lower than in the West ice pups, which is due to the higher amounts of blubber at birth on the West Ice newborn pups.

Moreover, since it appears that West Ice hooded seal newborns are born with a higher proportion of blubber than the Canadian ones, this suggests that the pups should be born with more quantities of energy stores. And in fact, that seems to be the case, it seems that neonates, in the present study, had roughly double the energy (18.6 MJ/kg, $n = 14$) than newborns off the coast of Labrador, Canada (10 MJ/kg, $n = 4$) (Table 6).
By being born with a thin blubber layer, and hence some reserves of energy, they get a possible head start to achieve the minimum energetic requirements to survive, in only 4 days (Oftedal et al., 1993).

4.2.2 Weaned seals

The four-day lactation period of the hooded seal is an intense stage for the pup and the mother. While the mother has to transfer enough energy during this time, the pup has to be able to assimilate the minimum nutrient requirements in order to survive the following fast. Therefore, hooded seals pups have a high gross energy efficiency of energy deposition, which is shared among other phocids (Iverson et al., 1993; Oftedal et al., 1993). Hooded seals are able to retain 84% of the ingested energy, mostly in the form of blubber (Oftedal et al., 1993). In the present study, the mean total energy of newborns and weaned seals differed by 44 %. Blaxter (1989) stated the efficiency of fattening is greater than the lean body mass gain. This can be observed in this study, where 91 % of the stored energy increase was due to the 63 % increase of the energy stored in blubber (Fig.6).

Since the main functions of muscles and viscera are not those of storing energy but to provide tissues for movement and body function, their energy densities are much lower than the blubber energetic density. Hence, the small contribution of muscles and viscera to the increase of the overall stored energy, was to be expected.

This means that in only three to four days, the hooded seals pups increased their total stored energy from 465.8 MJ to 1022.1 MJ. The energetic values estimated for the weaned pups in the present study were again higher than for the Canadian weaned pups (868 MJ) (Oftedal et al., 1993).

West Ice weaned pups had a higher mean weight of blubber than the Canadian pups, therefore the quantity of energy stored in the blubber was also higher. This variation in the amount of blubber deposition and energy deposition might be because hooded seals in the study by Oftedal et al. (1993) had reduced growth rate, which might have affected blubber deposition. It could be argued, that the seals in the present study had a similar growth rate, however, it is possible that the rate of mass gain presented in this paper is an underestimation, as stated before.

In the weaned hooded seals of this study, 78 % (Table 3) of the total energy stored was in the blubber and it was lower than in the Canadian weaned seals, where it was 86 %. The reduced growth rate of the Canadian weaned seals, may have also affected protein deposition, which in turn may have affected the allocation of energy proportions, increasing the amount blubber contributes to the total stored energy.

However, the Northwest Atlantic hooded seals had an almost identical blubber energy stored proportion to weaned harp (87 %). The viscera, though, were not considered when calculating protein percentage in that study (Oftedal et al., 1996), which increases the energy proportion of blubber. The percentage of energy stored in the blubber of weaned bluebacks pups is similar in grey seals (Iverson et al., 1993).

4.3 Theoretical fasting duration

The post weaning fast has been observed to last for about 4 weeks. During this time, pups lose 0.4 kg each day. By the end of this fast, pups have lost 29 % of the weaning mass (Bowen et al., 1987).

By estimating the amount of mobilizable energy, it was calculated that the average maximum fasting time for the weaned pups in this study was 73 days (Table 5). Based on these calculations weaned seals should be able to survive another month just on their energy reserves.

For the estimation of the maximum duration of the post weaning fast, the energy stores where related to the field metabolic rate (Equation 10). In this paper the term FMR is used to describe the BMR of the bluebacks, therefore it is defined as the total energy costs when the pup is inactive (on the ice), post-absorptive and in their thermo-neutral zone.

However, this estimated value of the duration of the post weaning fast is likely to be an overestimation of the real value. In nature, the situation of the post weaning fast is more complex since there are various aspects affecting a wild hooded seal pup, which were not taken into account when doing the estimations.

During the post weaning fast, hooded seal pups have been observed to have a short sedentary phase. They begin entering the water and diving just a few days shortly after weaning (Folkow et al., 2010). This increase in physical activity means that their metabolic rate increases, decreasing the energy stores and thus affecting the possible duration of their post weaning fast.

In addition, besides functioning as energy storage, the blubber layer has another function. Its other function is that of insulation, preventing heat loss and hypothermia in this arctic environment. Therefore, it has been suggested that fasting pups get their energy reserves not only from the deposited blubber layer, but also from the catabolism of proteins (Bowen et al., 1987).

Since more than 50% of the nitrogen depletion can lead to death (Young and Scrimshaw, 1971), it was assumed, that the maximum percentage of mobilizable proteins during the fast was 50 %. For the proportion of mobilizable blubber, it was taken into account that the insulating capacity may decrease when the blubber layer decreases below 1.5 cm (Nordøy and

Blix, 1985; Worthy, 1991). This means that for a mean blubber depth of 50 mm (*n*=4), a maximum of 70% of the total blubber energy at weaning can be mobilized.

Another variable that may play a role in the duration of the post weaning fast is the ice conditions. The yearly variation in the ice conditions of the arctic, changes the amount of suitable ice for hauling out. If there are less ice floes where pups can rest, then they are forced to spend more time in the water and the need to learn how to forage accelerates as well. Thus, their energy expenditure increases, and their energy stores are exhausted faster.

4.4 Maternal strategy of hooded seal mothers

Even though, males and females hooded seals aggregate during the breeding season, hooded seal mothers are the sole responsible for the postnatal care of the pups, males provide no assistance whatsoever (Bowen et al., 1992; Boness and Bowen, 1996). Most phocids mothers remain beside the pup during most of the lactation period. Hooded seal mothers remain on the ice with the pup the entire suckling period, without feeding (Bowen et al., 1987; Kovacs and Lavigne, 1992; Perry and Stenson, 1992). Therefore, the maintenance requirements of the mother and the milk production throughout the lactation period, will depend exclusively on the energy stored before parturition.

The extremely short lactation period may allow reduction of the metabolic costs of the mother and therefore, reach a more efficient nutrient transfer from the mother to the pup (Bowen et al., 1987; Oftedal et al., 1993).
This means that hooded seal mothers, in addition to having a brief period in which to transfer enough nutrients and energy to the pup, have limited energetic and nutrient resources throughout the suckling period. Thus, the development of a large and fat hooded seal pup before birth, is beneficial to this species. This prenatal nutrient and energy deposition on hooded seal appear to be substantial.

The amount of energy invested in the pups by the mothers will largely determine the survival of the offspring. Maternal energy investment was measured as energy deposition in the pup, but for intra- and interspecies comparison, where body size differ, maternal effort was expressed as energy deposition relative to metabolic mass of the mother (kilograms^{0,75}) (Equation 12). For the present study, it was assumed that maternal mass at parturition was on average 235 kg (Kovacs and Lavigne, 1992; Mellish et al., 1999) the same as in hooded seals of the Northwest Atlantic population since there was no data available for West Ice pregnant female hooded seals.

The relative maternal investment with respect to the total investment at weaning, appear to be different for both populations of hooded seals. Prenatal energy investment on the hooded seals of the Greenland Sea population was roughly 46 % of the total investment, higher than on the Canadian seals, where it was approximately 27 % (Oftedal et al., 1993) (Fig.8). Before birth, hooded seal mothers on this study deposited in the pups on average 7.8 $MJ/kg^{0.75}$. Canadian hooded seal females, on the other hand, deposited a lower amount of energy per metabolic size of the mother (4.9 MJ).

However, the inverse pattern of the prenatal investment can be seen during the lactation period, West Ice hooded seals mothers, deposited lower amount of energy throughout the lactation (9.3 $MJ/kg^{0.75}$) than the mothers of the Labrador Sea (12.9 $MJ/kg^{0.75}$). Even though, prenatal and postnatal maternal energy investment is not the same in both populations, it appears that by weaning, the mean maternal energy investment is similar for both, the West Ice mothers (17 $MJ/kg^{0.75}$) and the Canadian mothers (17.7 $MJ/kg^{0.75}$).Nevertheless, energy deposition for this population could be greater, since the suckling pups of the study carried out by Oftedal et al. (1993) had lower mean growth rates.

Though, it appears that both populations of hooded seals have different lactation strategies compared to other phocid species (Fig.8). The estimations of the deposition during the fetal development in harbor seals and bearded seal were similar to each other (Fig. 8), however they were lower than in hooded seal newborns. Harp seals appear to have the lowest prenatal deposition.

In addition to the diverse amounts of energy invested in these phocid seals, the relative investment during the prenatal phase and the postnatal phase, were different as well. In the present study, the energy deposited during the lactation period represented 55 % of the total energy deposition, at weaning. Hooded seals off the coast of St. Lawrence were reported to deposit 73% of the total energy during this stage. In harp seals, harbor seals and bearded seal energy deposition ranged from 83% to 93%.

There are some possible explanations for the wide variation between the values of both hooded seals. First of all, since the lactation period is so short, newborns collected at different times after birth, might introduce errors and lead to overestimations of the blubber content in newborns pups and thus affect the estimations of the amount of energy deposited during the fetal development stage.

Although, investment during fetal development and throughout the lactation period are different for all of the species, at weaning the amount of energy invested seems to fall in the same range 17 - 21 $MJ/kg^{0.75}$ (Fig.8). This might suggest that in order to produce a successful pup, at least among these North Atlantic phocids, a specific amount of energy in this range, must be incorporated in the tissues of the pups.

The different quantities of investment in relation to maternal metabolic size (Fig.8), suggests that there are two types of strategies during the lactation period, the head start strategy of the hooded seal and the postnatal investment of the other seals. Besides hooded seals, all the other phocids have longer lactation periods (12- 24 days), which means that they can take their time to transfer the minimum required energy.

Harbor and grey seals give birth on land, allowing a longer lactation period since it means that the whelping habitats have more stability and predictability (Bowen, 1991; Lydersen and Kovacs, 1999). On the other hand, bearded seals and harp seals give birth on the ice, under similar conditions as the hooded seals. However, lactation duration is not only correlated to habitat stability but it also may be correlated to ecological factors, neonate behavior and predation pressure (Lydersen and Kovacs, 1999; Schulz and Bowen, 2005).

Unlike most phocids, bearded seals are able to enter the water immediately after birth (Lydersen et al., 1996). Thus, they decrease the risk of premature separation form the mother and predation from polar bears.

Harp seals, on the contrary, not only give birth in the same unstable environments as the hooded seal but both, their timing of birth and efficiency of mass transfer are similar as well (Oftedal et al., 1989; Oftedal et al., 1996). Nonetheless, harp seals have a longer lactation period (12-13 days). It has been suggested that the reason why their lactation is longer is due two factors. First of all, harp seals have a lower fat content in their milk (40 %) (Lavigne et al., 1982). And second, the daily nursing rates of hooded seals are higher than in harp seals, which allows hooded seals to be weaned in a shorter period of time (Oftedal et al., 1989).

4.5 Energy deposition over time

For centuries, hooded seals have been hunted down intensively (Kovacs and Lavigne, 1986b). However, it was not until the 1920-ies, that the hunt for hooded seals of the Greenland Sea stock, increased considerably, when they became part of the commercial catch. After World War II, these hooded seals were commercially exploited at higher rates than the population could sustain. Consequently, regulatory measures were introduced 1958 for the hunt in the Jan Mayen and Denmark Strait areas.(Blix, 2005; Øigård et al., 2014). With management quotas that were imposed at Jan Mayen in 1971 and the previous reduction on catch effort, annual catches were successfully reduced (Kovacs and Lavigne, 1986b; Øigård et al., 2014). Nevertheless, the West Ice population suffered a substantial decrease from the 1940s and up to the early1980s.

Since 2006, hooded seals of the Greenland Sea stock have been protected, due to the small population size and the unprecise population estimates (ICES, 2006, 2016). Even though, it appears that the population has stabilized at a low level, the present population is only about 7% of what the population was in 1946 (Øigård et al., 2014; ICES, 2016). Currently, it is allowed only a modest harvest for scientific research. However, despite the fact that there is no more commercial harvest, it appears that the West Ice stock will keep declining in the future. Model prediction estimates suggested that the stock in the Greenland Sea would continue to decline in the upcoming years, by at least 8% (Øigård et al., 2014).

There have been several studies carried out with the object of explaining what could be causing the decline in abundance in the West Ice stock. One of these possible factors was a drop in female fertility (ICES, 2006). However, historically, the observed fecundity rates have been all around the same value. (ICES, 2016).

Epidemic diseases have also been suggested to contribute to the decline of West Ice hooded seals. Infections by *Brucella pinnipedialis* showed no effect on ovulation rate or neonatal body condition (Nymo et al., 2013).

Polar cod (*Boreogadus saida*), redfish (genus *Sebastes*), Greenland halibut (*Reinhardtius hippoglossoides*), and other flatfishes are important prey of hooded seals, which are also bycatches of commercial fisheries or are harvest for commercial purposes. Therefore, another factor that might be involved in the decline of the population is the competition with commercial fisheries for prey. However, little is known about how commercial fisheries affect prey availability (Frie et al., 2012).

In recent decades, there have been substantial evidence for climate warming by sea ice reduction, as well as air and sea temperatures increase (Laidre et al., 2008). Moreover, in the Arctic there has been not only a reduction of sea ice cover, but there has also been a decrease in sea ice thickness, in proportion of multiyear sea ice and its seasonal duration (Divine and Dick, 2006; Laidre et al., 2008; Kovacs et al., 2011; Laidre et al., 2015).
It was first noted by Vibe (1967) that climate change could impact the distribution and abundance of arctic marine mammals.

Hooded seals are an ice breeding species, who solely depend on ice for pupping, molting, and resting. Therefore, hooded seals are considered one of the arctic marine mammal most sensitive to climate change (Laidre et al., 2008).
In the central Greenland Sea, recent sea ice conditions are significantly different to those in the nineteenth century. The extent, concentration, type and longevity of the ice cover have also been affected (Wilkinson and Wadhams, 2005). For example, in previous decades the edge of the ice extended all the way to the Jan Mayen Island, but in the last decade it has only extended roughly 200 nautical miles to the west of the Jan Mayen Island (Øigård et al., 2014). It has been suggested that this thinning and reduction of the sea ice, may lead to an increase vulnerability of the weaned hooded seal pups to predation by polar bears and killer whales (*Orcinus orca*) (Øigård et al., 2014).
Moreover, besides a possible increase in predation, the ice could become more unstable and breakup could occur progressively earlier, as a result of climate warming. This in turn may lead to a decrease in pup survival, making climate change another possible factor involved in the decline in the West Ice population (Laidre et al., 2008) .

However, the shrinkage of the sea ice cover in the Arctic, could also be an explanation to the observed significant decline over the last 10 years in energy deposition by female hooded seals in the weaned pups (Fig.9). This decrease in ice could be affecting the amount of energy the mothers have stored for the lactation period.
The reduction of sea ice increases the potential biotope area of large boreal fish species, like cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*). This means that important hooded seal prey species, such as the Greenland halibut, may have more competition. It has

been shown that the abundance of Greenland halibut have decreased in the last decade (Fossheim et al., 2015). Other prey species may also be under increased competition or predation, as well as suffering of loss of habitat. Thus, it could be possible that prey availability has decreased, affecting the amount of energy the females can store by increasing foraging time and energy expenditure and decreasing food intake.

In addition to the possible negative effects on hooded seal prey, the remarkable retraction of the ice edge in the Greenland Sea could be also be contributing to the decrease in energy deposition. Unlike harp seals, hooded seals prefer to whelp in large heavy arctic ice floes (Sergeant, 1974). This means that with shrinkage of the ice edge in the central Greenland Sea, they are forced to whelp closer to the Greenland coast. A consequence of this, is that now hooded seal mothers may have to swim a greater distance when they return from their feeding grounds to the whelping areas. This may cause that the female hooded seal had increased energy expenditure and thus decrease quantity of stored energy for milk transfer to the pup.

It could be argued that the decrease in energy deposition in the weaned pups could be a reflection of female hooded seals giving birth progressively earlier on the season. If parturition was earlier on the season, then it would mean that the sampled weaned pups had already been fasting for a longer time. Hence, the estimated quantity of stored energy would appear to be decreasing. On the other hand, the amount of energy deposition in the weaned pups could also be an underestimation since it could be possible that the captured pups were not recently weaned.

However, I believe this is not the case for two reasons. First, it is known that hooded seals are weaned in 3 - 4 days (Bowen et al., 1985) and then remain sedentary for a short period of time (Folkow et al., 2010). Combined with the fact that most of the captured weaned seals were found in the same ice floes where they were born (as indicated by the presence of blood), were reluctant to enter the water and the presence and freshness of the umbilicus. Plus, with the exception of 2017, all hooded seal pups were captured during the same period, between 19-31 of March. All of this suggests that the pups were recently weaned.

Second, that peak whelping period for the Greenland Sea populations appear to be similar or slightly later than whelping peaks in previous decades. Results from the staging flights over the whelping patches suggest that the majority of hooded seal females whelped between 20 and 29 March in 2012, peaking on 24 of March (Øigård et al., 2014), similar to the peak period in 2007 (Øigård et al., 2010). Conversely, in 2005 whelping occurred between 17 and

23 of March, peaking five days earlier on March 19 (Salberg et al., 2008). However, whelping in 2012 was similar to the whelping observations in 1991 and 1994 (Øritsland, 1995).

Moreover, there are only two data points for newborns and weaned seals for each year, which means results are probably imprecise. Therefore, results should be taken as a first estimate on the condition of energy deposition in weaned pups.

However, if stored energy at weaning is in fact decreasing, could this reduction in energy stores be related to the current decline of the Greenland Sea population? Since mass and energy deposition at weaning, reflects the extent to which the pup is prepared to cope by itself with the upcoming adult life, it will determine the survival of the pup (Kovacs and Lavigne, 1986a). The decrease in energy deposition at weaning, may lead to a reduction in the post-weaning fast. This in turn may affect the physiological development of the pup since the ability to regulate metabolic processes and body oxygen stores increase during this time (Burns et al., 2004). It would be interesting to observe if the amount energy stores at weaning affect the timing when pups start to enter the water. Or if weaned hooded seals with larger energy stores have in fact higher chances of survival than those with lower quantities of energy stores after weaning.

5 Conclusion

Hooded seal pups are born in a highly precocial development state. The large amounts of blubber and energy deposited during the development stage contributes to the successful completion of the remarkably short lactation period of the hooded seals. Nevertheless, the results in the present study suggest that the West Ice hooded seals appear to be born with greater deposits of blubber than hooded seals of the Northwest Atlantic population. Furthermore, weaned seals appear to follow the same pattern, higher blubber proportion and energy deposition than the Northwest Atlantic population. However, by the end of lactation the investment of the females hooded seals of both stocks seems to be similar, which suggest that there might be a limitation on the amount of energy deposited per metabolic size of the mother. Moreover, it seems that there is a decreasing trend in the energy deposited by the female hooded seals by the end of lactation, which could be caused by the current climate change and could be contributing to the decline in abundance of this stock

6 References

Berta, A., 2017. Pinniped Evolution in: Bernd Würsig, J.T., Kit Kovacs (Ed.), Encyclopedia of Marine Mammals, Third ed. Elsevier Science, pp. 712-721.

Berta., A., Sumich., J.L., Kovacs, K.M., 2005. Pinniped Evolution and Systematics, Marine Mammals, Second ed. Elsevier Science, pp. 27-41.

Blaxter, K., 1989. Energy Metabolism in Animals and Man. Cambridge University Press.

Blix, A.S., 2005. Arctic Animals and Their Adaptations to Life on the Edge, illustrated ed. Tapir Academic Press.

Boness, D.J., Bowen, W.D., 1996. The Evolution of Maternal Care in Pinnipeds. BioScience 46, 645-654.

Bowen, W., 1991. Behavioural ecology of pinniped neonates, The behaviour of pinnipeds. Springer, pp. 66-127.

Bowen, W., Oftedal, O., Boness, D., 1985. Birth to weaning in 4 days: remarkable growth in the hooded seal, Cystophora cristata. Canadian Journal of Zoology 63, 2841-2846.

Bowen, W.D., Boness, D.J., Oftedal, O.T., 1987. Mass transfer from mother to pup and subsequent mass loss by the weaned pup in the hooded seal, Cystophora cristata. Canadian Journal of Zoology 65, 1-8.

Bowen, W.D., Oftedal, O.T., Boness, D.J., 1992. Mass and Energy Transfer during Lactation in a Small Phocid, the Harbor Seal (Phoca vitulina). Physiological Zoology 65, 844-866.

Burns, J.M., Clark, C.A., Richmond, J.P., 2004. The impact of lactation strategy on physiological development of juvenile marine mammals: implications for the transition to independent foraging. International Congress Series 1275, 341-350.

Coltman, D., Stenson, G., Hammill, M., Haug, T., Davis, C., Fulton, T., 2007. Panmictic population structure in the hooded seal (Cystophora cristata). Molecular Ecology 16, 1639-1648.

Costa, D.P., 1993. The relationship between reproductive and foraging energetics and the evolution of the Pinnipedia, Symp Zool Soc Lond, pp. 293-314.

Cottrell, P.E., Jeffries, S., Beck, B., Ross, P.S., 2002. Growth and development in free-ranging harbor seal (phoca vitulina) pups from southern British Columbia, Canada . Marine Mammal Science 18, 721-733.

Divine, D.V., Dick, C., 2006. Historical variability of sea ice edge position in the Nordic Seas. Journal of Geophysical Research: Oceans (1978–2012) 111.

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

Folkow, L.P., Mårtensson, P.-E., Blix, A.S., 1996. Annual distribution of hooded seals (Cystophora cristata) in the Greenland and Norwegian Seas. Polar Biology 16, 179-189.

Folkow, L.P., Nordøy, E.S., Blix, A.S., 2010. Remarkable development of diving performance and migrations of hooded seals (Cystophora cristata) during their first year of life. Polar Biology 33, 433-441.

Fossheim, M., Primicerio, R., Johannesen, E., Ingvaldsen, R.B., Aschan, M.M., Dolgov, A.V., 2015. Recent warming leads to a rapid borealization of fish communities in the Arctic. Nature Climate Change 5, 673.

Frie, A.K., Stenson, G.B., Haug, T., 2012. Long-term trends in reproductive and demographic parameters of female Northwest Atlantic hooded seals (Cystophora cristata): population responses to ecosystem change? Canadian Journal of Zoology 90, 376-392.

Grav, H.J., Blix, A.S., 1976. Brown adipose tissue—a factor in the survival of harp seal pups. Canadian journal of physiology and pharmacology 54, 409-412.

ICES, 2006. Report of the Working Group on ICES/NAFO Working Group on Harp and Hooded Seals (WGHARP),12-16 June 2006, ICES Headquarters., pp. ICES CM 2006/ACFM:2032- 2028 pp. .

ICES, 2016. Report of the ICES/NAFO/NAMMCO Working Group on Harp and Hooded Seals (WGHARP), 26-30 September 2016, 26-30 September 2016, ICES HQ, Copenhagen, Denmark. , pp. ICES CM 2016/ACOM:2021-2085 pp. .

Iverson, S., Hamosh, M., Bowen, W., 1995. Lipoprotein lipase activity and its relationship to high milk fat transfer during lactation in grey seals.

Iverson, S.J., Bowen, W.D., Boness, D.J., Oftedal, O.T., 1993. The Effect of Maternal Size and Milk Energy Output on Pup Growth in Grey Seals (Halichoerus grypus). Physiological Zoology 66, 61-88.

Kovacs, K., Lavigne, D., 1992. Mass-transfer efficiency between hooded seal (Cystophora cristata) mothers and their pups in the Gulf of St. Lawrence. Canadian Journal of Zoology 70, 1315-1320.

Kovacs, K.M., 2018. Hooded Seal: Cystophora cristata, Encyclopedia of Marine Mammals (Third Edition). Academic Press, pp. 477-480.

Kovacs, K.M., Lavigne, D., 1985. Neonatal growth and organ allometry of Northwest Atlantic harp seals (Phoca groenlandica). Canadian Journal of Zoology 63, 2793-2799.

Kovacs, K.M., Lavigne, D., 1986a. Maternal investment and neonatal growth in phocid seals. The Journal of Animal Ecology, 1035-1051.

Kovacs, K.M., Lavigne, D.M., 1986b. Cystophora cristata. Mammalian Species, 1-9.

Kovacs, K.M., Lydersen, C., Overland, J.E., Moore, S.E., 2011. Impacts of changing sea-ice conditions on Arctic marine mammals. Marine Biodiversity 41, 181-194.

Kuzawa, C.W., 1998. Adipose tissue in human infancy and childhood: An evolutionary perspective. American Journal of Physical Anthropology 107, 177-209.

Laidre, K.L., Stern, H., Kovacs, K.M., Lowry, L., Moore, S.E., Regehr, E.V., Ferguson, S.H., Wiig, Ø., Boveng, P., Angliss, R.P., Born, E.W., Litovka, D., Quakenbush, L., Lydersen, C., Vongraven, D., Ugarte, F., 2015. Arctic marine mammal population status, sea ice habitat loss, and conservation recommendations for the 21st century. Conservation Biology 29, 724-737.

Laidre, K.L., Stirling, I., Lowry, L.F., Wiig, Ø., Heide-Jørgensen, M.P., Ferguson, S.H., 2008. Quantifying the sensitivity of arctic marine mammals to climate-induced habitat change. Ecological Applications 18, S97-S125.

Lavigne, D., Stewart, R., Fletcher, F., 1982. Changes in composition and energy content of harp seal milk during lactation. Physiological Zoology 55, 1-9.

Lavigne, D.M., Innes, S., Worthy, G.A.J., Kovacs, K.M., Schmitz, O.J., Hickie, J.P., 1986. Metabolic rates of seals and whales. Canadian Journal of Zoology 64, 279-284.

Lestyk, K.C., Folkow, L.P., Blix, A.S., Hammill, M.O., Burns, J.M., 2009. Development of myoglobin concentration and acid buffering capacity in harp (Pagophilus groenlandicus) and hooded (Cystophora cristata) seals from birth to maturity. Journal of Comparative Physiology B 179, 985.

Liwanag, H.E., Berta, A., Costa, D.P., Abney, M., Williams, T.M., 2012. Morphological and thermal properties of mammalian insulation: the evolution of fur for aquatic living. Biological Journal of the Linnean Society 106, 926-939.

Lydersen, Kovacs, K.M., 1999. Behaviour and energetics of ice-breeding, North Atlantic phocid seals during the lactation period. Marine Ecology Progress Series, 265-281.

Lydersen, C., Kovacs, K.M., Hammill, M.O., Gjertz, I., 1996. Energy intake and utilisation by nursing bearded seal (Erignathus barbatus) pups from Svalbard, Norway. Journal of Comparative Physiology B 166, 405-411.

McLean, J.A., Tobin, G., 1987. Animal and Human Calorimetry, illustrated, reprint ed. Cambridge University Press.

Mellish, J.E., Iverson, S.J., Bowen, W.D., Hammill, M.O., 1999. Fat transfer and energetics during lactation in the hooded seal: the roles of tissue lipoprotein lipase in milk fat secretion and pup blubber deposition. Journal of Comparative Physiology B 169, 377-390.

Nordøy, E.S., Blix, A.S., 1985. Energy sources in fasting grey seal pups evaluated with computed tomography. American Journal of Physiology-Regulatory, Integrative and Comparative Physiology 249, R471-R476.

Nymo, I.H., Tryland, M., Frie, A.K., Haug, T., Foster, G., Rødven, R., Godfroid, J., 2013. Age-dependent prevalence of anti-Brucella antibodies in hooded seals Cystophora cristata. Diseases of Aquatic Organisms 106, 187-196.

Oftedal, O.T., Boness, D.J., BOwEN, W.D., 1988. The composition of hooded seal (Cystophora cristata) milk: an adaptation for postnatal fattening. Canadian Journal of Zoology 66, 318-322.

Oftedal, O.T., Boness, D.J., Tedman, R.A., 1987. The behavior, physiology, and anatomy of lactation in the pinnipedia, Current mammalogy. Springer, pp. 175-245.

Oftedal, O.T., Bowen, D., Widdowson, E.M., Boness, D.J., 1989. Effects of suckling and the postsuckling fast on weights of the body and internal organs of harp and hooded seal pups. Neonatology 56, 283-300.

Oftedal, O.T., Bowen, W.D., Boness, D.J., 1993. Energy Transfer by Lactating Hooded Seals and Nutrient Deposition in Their Pups during the Four Days from Birth to Weaning. Physiological Zoology 66, 412-436.

Oftedal, O.T., Bowen, W.D., Boness, D.J., 1996. Lactation Performance and Nutrient Deposition in Pups of the Harp Seal, Phoca groenlandica, on Ice Floes off Southeast Labrador. Physiological Zoology 69, 635-657.

Oftedal, O.T., Bowen, W.D., Widdowson, E.M., Boness, D.J., 1991. The prenatal molt and its ecological significance in hooded and harbor seals. Canadian Journal of Zoology 69, 2489-2493.

Øigård, T.A., Haug, T., Nilssen, K.T., 2014. Current status of hooded seals in the Greenland Sea. Victims of climate change and predation? Biological Conservation 172, 29-36.

Øigård, T.A., Haug, T., Nilssen, K.T., Salberg, A.-B., 2010. Estimation of pup production of hooded and harp seals in the Greenland sea in 2007: reducing uncertainty using generalized additive models.

Øritsland, T., Øien, N, 1995. Aerial Surveys of Harp and Hooded Seal Pubs in the Greenland Sea pack ice, in: A. Schytte Blix, L.W., Ø. Ulltang (Ed.), Whales, Seals, Fish and Man. Elsevier, Amsterdam, pp. 77-87.

Perry, E.A., Stenson, G.B., 1992. Observations on Nursing Behaviour of Hooded Seals, Cystophora cristata. Behaviour 122, 1-10.

Salberg, A.B., Haug, T., Nilssen, K.T., 2008. Estimation of hooded seal (Cystophora cristata) pup production in the Greenland Sea pack ice during the 2005 whelping season. Polar Biology 31, 867-878.

Schulz, T.M., Bowen, W.D., 2005. The evolution of lactation strategies in pinnipeds: a phylogenetic analysis. Ecological Monographs 75, 159-177.

Sergeant, D.E., 1974. A rediscovered whelping population of hooded seals Cystophora cristata Erxleben and its possible relationship to other populations. Polarforschung 44, 1-7.

Sergeant, D.E., 1976. History and present status of populations of harp and hooded seals. Biological Conservation 10, 95-118.

Shepeleva, K., 1973. Adaptation of Seals to Life in the Arctic, in: Sokolov, V.E., Shepeleva, V.K. (Eds.), Morphology and ecology of marine mammals; seals, dolphins, porpoises. J. Wiley, New York, pp. viii, 232 p.

Spray, C.M., Widdowson, E.M., 1950. The Effect of Growth and Development on the Composition of Mammals. British Journal of Nutrition 4, 332-353.

Vibe, C., 1967 Arctic animals in relation to climatic fluctuations. Reitzel, København.

Widdowson, E.M., 1950. Chemical Composition of Newly Born Mammals. Nature 166, 626.

Wilkinson, J.P., Wadhams, P., 2005. A Method of Detecting Change in the Ice Conditions of the Central Greenland Sea by the Whelping Locations of Harp Seals. Journal of Climate 18, 1216-1226.

Worthy, G.A., Lavigne, D., 1983. Changes in energy stores during postnatal development of the harp seal, Phoca groenlandica. Journal of Mammalogy 64, 89-96.

Worthy, G.A.J., 1991. Insulation and thermal balance of fasting harp and grey seal pups. Comparative Biochemistry and Physiology Part A: Physiology 100, 845-851.

Young, V.R., Scrimshaw, N.S., 1971. The physiology of starvation. Scientific American 225, 14-21.