

Evaluation of condition indices relating to seasonal changes
and diet of harp seals, Phoca groenlandica Erxleben 1777.

by

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ABSTRACT

Indices of nutritional condition and diet were evaluated in harp seals Phoca groenlandica (n=124) obtained from hunters in Hudson Strait and the Gulf of St. Lawrence, December 1988 to October 1990. In winter seals, blubber and the lean, eviscerated carcass contributed 90% and 9% of total body lipids, respectively (n=9). Lipid was distributed homogeneously throughout the blubber in a late February sample of mature males (n=6). Blubber thickness and girth at 50% of length showed the strongest correlation to fat stores, but the direct measurement of sculp (i.e. skin with attached blubber) and total body mass may be necessary to show variations in nutritional condition. While percent blubber of total body mass indicates the state of thermal balance, seasonal fluctuations in the mass of both sculp and the lean carcass (with viscera) limit its usefulness as an index of energy stores. Sculp and core mass in females increased from autumn (49.6 ± 2.7 kg and 49.4 ± 3.5 kg, respectively, $\text{mean} \pm \text{1se}$) to winter (57.4 ± 1.9 kg and 57.9 ± 2.5 kg, respectively). Mature males were observed to significantly increase their blubber mass from early to late winter ($p < 0.05$). Muscle and liver lipid content varied seasonally in both sexes, and were highest in a sample of females one month post-partum which were feeding very intensively ($2.0 \pm 0.3\%$ and $7.3 \pm 1.4\%$, respectively, $\text{mean} \pm \text{1sd}$). These females had reduced blubber mass and blubber lipid content, but the highest observed core mass, the latter being significantly heavier than in autumn (64.9 ± 2.9 kg, $\text{mean} \pm \text{1se}$, $p < 0.05$). Unequal sample size of males and females restricted statistical analysis of condition indices. Changes in nutritional condition reflect seasonal variation in feeding intensity. Capelin (Mallotus villosus) is the preferred food item, where available, and was the primary prey in both the St. Lawrence River estuary and Hudson Strait. Harp seals on their southward migration fed less intensively than in other seasons, but on a greater variety of fish and plankton.

RÉSUMÉ

J'ai étudié les indices d'état nutritif, ainsi que la diète de 124 phoques du Groënland obtenus par des chasseurs dans le détroit d'Hudson et le Golfe du St-Laurent, de décembre 1988 à octobre 1990. En hiver, la couche adipeuse et la carcasse (muscles, squelette sans viscera) ont contribué respectivement à 90% et 9% du total des lipides corporels. Les lipides étaient distribués d'une façon homogène dans la couche graisseuse parmi un échantillon de six mâles matures pris vers la fin de février. L'épaisseur de la couche graisseuse et la circonférence à la mi-longueur étaient fortement corrélées avec la réserve de gras. Cependant, le poids de l'écorce (i.e. la peau avec la graisse) et le poids total du corps indiquaient mieux l'état nutritif. Le rapport du poids de la couche graisseuse au poids total indique l'état de l'équilibre thermal, mais les fluctuations saisonnières dans le poids de l'écorce et de la carcasse (avec viscera) nuisent à ces mesures comme indices nutritifs. Le poids de l'écorce et la carcasse chez les femelles ont augmenté de l'automne (49.6 ± 2.7 kg et 49.4 ± 3.5 kg, respectivement, moyenne $\pm$ erreur type) à l'hiver (57.4 ± 1.9 kg et 57.9 ± 2.5 kg, respectivement). Les mâles matures ont augmenté significativement le poids de leur couche graisseuse, du début à la fin de l'hiver ($p < 0.05$). Les lipides contenus dans les muscles et le foie variaient d'une façon saisonnière chez les deux sexes. Ils ont atteint leur maximum ($2.0 \pm 0.3\%$ et $7.3 \pm 1.4\%$, muscles et foie, respectivement, moyenne $\pm$ écart-type) dans un échantillon de femelles un mois après la mise-bas; ces bêtes se nourrissaient intensivement durant cette période. Il y avait une réduction dans le poids et le contenu lipides de ces mêmes femelles mais le poids de leurs carcasses était au maximum observé; significativement plus lourd qu'à l'automne (64.9 ± 2.9 kg, moyenne $\pm$ erreur-type, $p < 0.05$). L'analyse statistique des indices de condition a été empêchée par l'inégalité du nombre d'échantillons entre mâles et femelles. Les changements

dans l'état nutritif reflètent les variations saisonnières d'alimentation. Le capelan (Mallotus villosus) est la proie préférée du phoque du Groënland, la plus importante dans l'estuaire du fleuve St-Laurent et dans le détroit d'Hudson. Les phoques du Groënland se nourrissent moins et se servent d'une plus grande variété de nourriture lors de leur migration vers le sud.

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NOTE REGARDING PUBLICATION

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CHAPTER I

GENERAL INTRODUCTION

GENERAL INTRODUCTION

The harp seal (Phoca groenlandica Erxleben 1777) is the most abundant pinniped inhabiting the waters of the North Atlantic, and the second or third most abundant worldwide (King 1983; Riedman 1990; Sergeant In press). Three populations exist: two are located in the northeast Atlantic and the third, in Canadian waters, is further subdivided into two main breeding herds (Ronald and Healey 1981). The larger occurs off the coast of southern Labrador (the 'Front' herd) and has twice the population of the herd in the Gulf of St. Lawrence (Sergeant In press). Some mixing of stocks occurs within the two northeastern populations and the two Canadian herds, but crossover between the east and west Atlantic populations is rare (Sergeant 1973a).

The long annual migrations of the harp seal are related to patterns of ice formation and influence the seasonal variation in diet and body condition. While not frequenting areas of fast-ice, the harp seal is found in close association with pack ice in most seasons (Sergeant 1965), hence the present sub-generic designation of *Pagophilus*, or 'ice-lover'. During spring, harp seals moult and spend much of the time hauled out on the ice and appear to feed only intermittently (Sergeant 1973b). As the ice melts, they begin their northward migration and by summer large numbers arrive on the western coast of Greenland. Most juveniles remain in this region for the summer, but many mature seals enter

the waters of the eastern and high arctic and, in smaller numbers, Hudson Strait and Hudson Bay (Mansfield 1963; Sergeant 1965).

Considerable seasonal variation in feeding habits and fat reserves is observed in the harp seal. Reduced feeding in spring, the northward migration, and for females, the cost of lactation, all contribute to the depletion of energy stores. By summer, harp seals are very lean, weighing 100 kg, 30 kg lighter than in winter (Sergeant 1973b). At this time, they feed heavily and begin to restore lost energy reserves. Harp seals are known to feed on a wide variety of fish and plankton. In summer, capelin (Mallotus villosus), arctic cod (Boreogadus saida) and crustacea are most frequent, the relative importance of prey species depending on local abundance (Sergeant 1973b; Smith et al. 1979; Lydersen et al. 1989; Finley et al. 1990). During the southward migration and in winter and spring in the estuary of the St. Lawrence, harp seals feed most heavily on capelin (Sergeant 1973b; 1976; Murie 1984; Foy et al. 1981). The replenishment of energy stores begun in the arctic continues through the autumn and winter, and by late winter harp seals are very fat (Sergeant 1973b).

In late February, harp seals begin to congregate on the pack ice for parturition and mating. In the Gulf of St. Lawrence, the mean date of pupping is 2 March (Stewart et al. 1989), slightly

later at the Front (Sergeant 1976). The pup grows rapidly during the 12 days of lactation, increasing from 10 kg at birth to 35 kg when weaned (Kovacs and Lavigne 1985). Mating occurs at this time, although implantation of the embryo does not occur until August (Stewart et al. 1989). The rapid increase in mass of the pup is possible because of the high energy content of the milk, which ranges from 29 to 50% lipid (Sivertsen 1941; Cook and Baker 1969; Stewart et al. 1983). Consequently, females lose body fat at a rate of 3.17 kg/day (Stewart and Lavigne 1984). The accessibility of harp seals on the breeding grounds of the Gulf of St. Lawrence has enabled detailed study of the energetics of lactation and the post-weaning fast in pups (Worthy and Lavigne 1983a; 1983b; 1987; Worthy 1987). Following weaning and mating, a brief but intensive period of feeding is known to occur in the St. Lawrence River estuary (Sergeant 1973b).

The seasonal variations in feeding and fattening have important implications for applied aspects of the biology of the harp seal. Depressed commercial fish stocks combined with an increasing harp seal population (Roff and Bowen 1983; 1986) emphasize the importance of monitoring diet in harp seals, particularly in areas which have not been intensively studied. However, Lavigne et al. (1985) estimate that harp seals obtain 54% of their annual energy intake in waters north of Hamilton Inlet. While the fat of marine mammals serves many functions (Scholander 1950; Bryden 1968; Pond 1978), temporal fluctuations

in blubber mass may be useful as an indication of prey abundance and variations in the density of the seal population (Stewart and Lavigne 1984; Smith and Hammill 1987). Organochlorine contaminants have been found in the fatty tissues of harp seals and reflect levels of pollution in the marine environment (e.g. Addison et al. 1973; Addison and Smith 1974; Ronald et al. 1984; Addison 1989). Knowledge of the seasonal variation in fat reserves enables a more detailed interpretation of the total burden of contaminants in marine mammals.

In the harp seal, as with other seal species, nutritional condition has often been studied only incidentally (McLaren and Smith 1985). The link between seasonal variation in energy stores and feeding habits has not been studied in detail with data most lacking for specimens from the arctic. In Chapter II of the thesis, I evaluate various body measurements to determine which best reflect nutritional condition in the harp seal. In Chapter III, stomach contents, percent lipid in muscle, liver and blubber and total body and blubber mass are evaluated to investigate seasonal variation in diet and nutritional condition.

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CHAPTER II

Evaluation of indices of nutritional condition
in the harp seal, Phoca groenlandica.

Abstract

Indices of nutritional condition were evaluated in harp seals Phoca groenlandica (n=119) by examining body measurements and carcass and tissue lipid content. Specimens were collected from hunters in Hudson Strait and the Gulf of St. Lawrence between December 1988 and March 1990. Ninety percent of total body lipid in 9 winter animals was in the blubber and the distribution of lipid throughout the blubber was found to be homogeneous. Blubber thickness was most variable dorsally and greatest at 50% of length, which coincides with the position of maximum girth. Condition indices based on girth/length and blubber thickness show the strongest correlation to both blubber mass and percent blubber content when measured at this position. The direct measurements of sculp, core and total body mass are much more accurate, however, and may be necessary to show significant differences in nutritional condition. Percent blubber content is valuable as an indicator of the state of insulation, but seasonal variation in both core and blubber mass limits its usefulness as an index of energy reserves. Since blubber contains the greatest amount of lipids, sculp or blubber mass adjusted for standard length cubed is the best index of stored energy.

INTRODUCTION

Nutritional condition is important in determining the size and health of animal populations. For terrestrial homeotherms, condition affects survival during times of environmental stress and can influence reproductive rates (Young 1976; Hanks 1981; Thomas 1982). In marine mammals, the level of fat reserves, stored principally in the blubber, has been considered the best indication of nutritional condition (Lockyer 1986; Read 1990; Ryg et al. 1990a). The fat deposits serve as an energy store, a source of buoyancy and streamlining and as insulative protection against the high thermal conductivity of water (Scholander et al. 1950; Pond 1978; Worthy and Lavigne 1987; Ryg et al. 1988). As with terrestrial animals, condition may influence reproductive success and affect survivorship of offspring in marine mammals (Stewart and Lavigne 1984; Lockyer 1986; Smith 1987; Doidge and Croxall 1989). Because of the lipo-philic nature of organochlorine compounds, study of contaminants in marine mammals should consider seasonal, sexual and age-specific variation in fat deposits (Addison et al. 1973; Addison and Smith 1974; Ronald et al. 1984; Addison 1989).

Despite its importance, body condition has often been studied only incidentally in seals (reviewed in McLaren and Smith 1985). Traditionally, xiphosternal blubber thickness (including

skin) and girth/length*100 have been used to estimate body condition (McLaren 1958; American Society of Mammalogists 1967). Seasonal and sexual variations in these indices have been observed in harp seals (Sergeant 1973), ringed seals Phoca hispida (McLaren 1958; Smith 1987) and harbour seals Phoca vitulina (Pitcher 1986). Seasonal changes using total body mass or percent blubber of body mass (i.e. percent blubber content) as indicators of body condition have been reported (Boulva and McLaren 1979; Fedak and Anderson 1982; Stewart and Lavigne 1984; Bowen et al. 1987; Hammill 1987). Lockyer et al. (1985) suggested that blubber thickness at its most variable site might be the best index of condition in fin (Balaenoptera physalus) and sei (Balaenoptera borealis) whales. Ryg et al. (1988) found blubber in the ringed seal most variable dorsally, at a position sixty percent of standard length, posterior to the snout (i.e. reference length 0.6, $RL_{0.6}$).

To interpret condition data correctly, measurements such as standard length, girth and mass must be carefully defined, but this is often not done (reviewed in McLaren and Smith 1985). The American Society of Mammalogists (1967) recommended girth be measured at the axilla and that xiphosternal blubber thickness should include the thickness of the skin. Maximum girth and blubber thickness excluding skin are now commonly measured which leads to confusion in the literature. Errors in condition indices based on total body mass occur if corrections are not made for

the mass of the stomach contents or the foetus. Variable blood loss following collection adds considerable error due to the large volume of blood in seals (St. Aubin et al. 1978).

Some attempts have been made to examine the value of blubber thickness and girth/length*100 as indices of nutritional condition (Pitcher 1986; Ryg et al. 1990a). Generally, authors have used percent blubber content or percent sculp (i.e. skin with blubber attached) of total body mass as the standard for comparison. Ryg et al. (1990a) note that fat stores in the core (carcass and viscera) should also be considered to better estimate nutritional condition. Hammill (1987) found a different index (sculp mass/maximum girth²) was most highly correlated to percent total body lipid in ringed seals. Interpretation of data on percent blubber content and other condition indices has been based on the assumptions that the mass of the core is relatively constant in mature animals (Stewart and Lavigne 1984; Ryg et al. 1990b) and that the percent lipid in the blubber and other tissues does not vary significantly with season.

Because of the recognition that nutritional condition reflects changing environmental conditions and may also reflect the health of the marine environment in general, it is important to evaluate indices of condition and some of the associated assumptions. Here, I use body measurements and the biochemical analysis of total lipid in the carcass and various tissues to

establish which index or indices best reflect nutritional condition in the harp seal.

MATERIALS AND METHODS

Harp seals (n=119) were obtained from hunters at various sites in Quebec between December 1988 and March 1990 (Figure 1, Table 1). Specimens were taken by shooting at Les Escoumins (December 1988 to April 1989, n=51), Salluit (September to October 1989, n=11) and Harrington Harbour (December 1989, n=17). Male specimens from Iles de la Madeleine were included in the analyses (late February/early March 1989, n=23, and 1990, n=17). Carcasses from Les Escoumins were frozen before being shipped to Montreal for dissection in the laboratory. All other specimens were processed in the field.

Carcasses were weighed whole and to the nearest kilogram, except for those over 90 kg taken at Salluit and Harrington Harbour where core and sculp were weighed separately. Total body mass was corrected for the mass of stomach contents and foetus, but not for blood loss. Standard measurements were made on all seals (American Society of Mammalogists 1967). Measurements of blubber thickness did not include the thickness of the skin. Additional girth measurements were taken around the snout and head, at the maximal position and at 10 cm intervals from the snout to the anus. The sculp, not including flippers, was separated from the core and weighed. During laboratory dissections, the sculp was then stretched to standard length and placed on a flat table. Blubber thickness was measured to the

nearest millimetre at 10 cm intervals along the length and width using the vernier extension of precision callipers. Sculp width was also measured at the 10 cm intervals (Ryg et al. 1988). I observed that the thickest part of the sculp lies next to the vertebral column and it was taken to be the true centre line of the sculp. The blubber was separated from the skin and blubber mass determined by subtraction. For specimens weighed whole, core mass was calculated as total body mass minus sculp mass. The viscera were examined visually for fat deposits. In the laboratory, organs were weighed to the nearest gram (Sartorius Co., Model E5500S, Germany).

Age was assigned by counting annular growth rings in the dentine of thin transverse sections of a lower canine tooth (Bowen et al. 1983). If by the third reading, 2 identical values were not obtained, results from the 3 readings were averaged. Reported age refers to age as at the last anniversary, based on a mean parturition date in the Gulf of St. Lawrence of 2 March (Stewart et al. 1989). Ovaries were sectioned and examined to determine reproductive status. Females with at least one corpus luteum or corpus albicans present on the ovaries were considered sexually mature (Fisher 1954; McLaren 1958). Four of 36 sexually mature females examined were barren and not included in the statistical analyses of seasonal variations in body condition (ages: 8,16,23,31 years). Males which had attained a length of 152 cm were classified as mature (Laws 1956).

Sternal blubber, liver, hip and back muscle samples were analyzed for total lipid (n=79). To determine the distribution of lipid in the blubber, additional blubber samples were collected from 6 mature males at Iles de la Madeleine, 25 and 27 February, 1990. Five body sites were selected for analysis: the neck (lateral), sternum, hip, and dorsal positions at RL_{0.33} and RL_{0.6}. Samples were wrapped in aluminium foil and frozen to -20°C.

Total body lipids were estimated from the carcass and viscera (excluding stomach, foetus and reproductive organs) of 9 specimens (males n=6, females n=3). These frozen carcasses were ground in a large animal grinder (Autio Co., Model 301B, Indianapolis, Indiana), then reground three times to ensure full homogenization. A skin sample from one animal was cut while frozen with a band saw then ground in the large animal grinder. Skin proved very difficult to process and no further sub-samples were made. Viscera were frozen separately and homogenized in a commercial blender (Waring Co., Model CB-5, Winsted, Connecticut). Carcass and viscera sub-samples were freeze-dried (Virtis Co., Model 10-020, Series 1025, Gardiner New York), then reground in a kitchen blender. Muscle and liver samples were freeze-dried and ground by mortar and pestle. I found that cutting muscle samples across the grain kept fibres relatively

short and facilitated pulverization. Water content was estimated as the difference between wet and freeze-dried weights.

Total lipid was extracted by micro-soxhlet refluxing for 4 hours with chloroform-methanol (2:1, by volume, Giese 1967). The crude extract was washed and rinsed twice with 0.29 percent NaCl (Folch et al. 1957), rinsed twice again with distilled water and the pure extract oven dried at 60°C for 24 hours. Percent lipid in the subsamples was determined gravimetrically from the difference of pre and post extraction weights (Sartorius Co., Model R160P, Germany). Dried liver, muscle, skin, viscera and carcass subsamples of approximately 100 mg were used. To minimize handling and potential loss of lipid, extraction from blubber was performed on 300 mg subsamples of the wet tissue, cut from the centre of the frozen sample. Extractions were repeated twice on liver and muscle samples, three times on blubber and five times for each of the skin, carcass and viscera samples.

To test homogeneity of lipid in the blubber, samples were taken at 3 depths within each of the 5 body sites. Since blubber lacked the distinctive zonation found in fin (Balaenoptera physalus) and sei (Balaenoptera borealis) whales (Lockyer et al. 1984), the blubber column was divided into 3 equal divisions. To reduce the chance of error due to oxidation of lipids, approximately 0.5 cm of blubber was trimmed from the outer and inner surfaces of the whole tissue block. These samples were

collected in the field at a temperature of -15°C , were frozen immediately and did not show discoloration at the edges as was observed in blubber samples collected in the laboratory.

For the purpose of analyzing seasonal changes, mature specimens were grouped as follows: Les Escoumins winter (25 December, 1988 to 21 January, 1989), Iles de la Madeleine 1989 (4 March to 8 March, 1989), Les Escoumins April (14 and 16 April, 1989), Salluit (30 September to 4 October, 1989), Harrington Harbour (6 December to 21 December, 1989) and Iles de la Madeleine 1990 (25 February to 10 March, 1990; Table 2).

Statistical tests were performed using the Statistical Analysis System for personal computers (SAS Institute Inc. 1988, version 6.03). Means of length, age, and date of collection involving two groups were compared using Proc t-test and those of three or more means by analysis of variance with Proc GLM. When variances were not homogeneous (F-test, Snedecor and Cochran 1967), means were compared using Proc t-test for unequal variances. Differences in means were located using Duncan's multiple range test (Proc GLM). Tests for normality were performed using Proc Univariate. In the split-plot design (Proc GLM) used to analyze the data on homogeneity of lipid in the blubber, individual seals represented blocks, body site the main plot effect, blubber depth the sub-plot effect and replicates the sampling units. For each specimen, mean percent lipid in each

tissue was calculated from all replicates and the single value included in the statistical tests. A paired t-test (Proc Means) was used to test the difference in percent lipid between back and hip muscle samples. Total body lipid was estimated by separately determining the percent lipid in each of the four component body parts (blubber, carcass, viscera, and skin) and then multiplying by the mass of each component. Percent lipid of total mass was obtained by dividing total body lipid by corrected body mass.

Sculp widths and blubber thickness were interpolated linearly from the 10 x 10 cm grid to reference lengths at 0.2, 0.3,...0.8 at dorsal, ventral, right and left lateral positions (i.e. 28 locations). Interpolated sculp widths were compared to corresponding girth measurements with a paired t-test (Proc Means). Variance associated with blubber thickness at each RL was calculated using Proc Means.

A single factor analysis of covariance (Proc GLM) was used to compare body measurements which might be influenced by body size. Standard length was used as the single covariate for linear measurements, and to maintain dimensional equality standard length³ was used for mass (Stahl 1962). Homogeneity of slopes was established as a preliminary requirement for further analysis and comparison (Zar 1984) and least square means were calculated to isolate differences between the group means and elevations. To

fit predictive power functions, natural log transformations were performed on the data.

Simple and multiple linear regression equations were fitted using the Proc Reg procedure. Pearson Correlation Coefficients (r) were calculated with Proc Corr. Percent blubber content was predicted by blubber thickness to girth ratios, by separately estimating component masses, and by subtracting predicted skin mass from measured sculp mass. Estimates calculated by these methods were compared to observed values for 49 specimens (Proc Corr).

RESULTS

Standard length varied significantly between the sexes ($t=-2.23$, $p<0.05$, males $168.1 \text{ cm} \pm 7.0$ $n=68$, females $164.6 \text{ cm} \pm 7.2$ $n=30$, mean $\pm$ lsd (cm)). With sexes considered separately, no significant difference in standard length was observed between the seasonal groups (males $F_{3,62}=1.82$, $p>0.05$; females $F_{3,26}=2.33$, $p>0.05$; Figure 1). Females were significantly older than males ($t=1.99$, $df=91$, $p=0.0493$; 14.0 ± 6.6 , 11.5 ± 5.4 , mean $\pm$ lsd (years), respectively).

The position of maximum girth was more posterior in females than in males ($t=3.54$, $df=75$, $p<0.001$; females $RL_{0.51} \pm 0.04$ $n=40$, males $RL_{0.48} \pm 0.04$ $n=37$, mean $\pm$ lsd). When seasonal groups were considered separately, the difference between sexes was significant for specimens from Les Escoumins in winter alone ($t=2.99$, $df=32$, $p<0.01$); however, sample sizes from Harrington Harbour and Salluit for mature animals were very small. The position of maximum girth did not vary seasonally for either males ($F_{2,24}=0.49$, $p>0.05$) or females ($F_{3,25}=0.81$, $p>0.05$). No significant difference in the position of maximum girth was observed between the sexes in juveniles collected at Harrington Harbour ($t=0.16$, $df=9$, $p>0.05$). The mean position of maximum girth, with data for the sexes and all ages combined, was $RL_{0.49} \pm 0.07$ (mean $\pm$ lsd, $n=75$). This corresponds to the site of

maximum blubber thickness. The mean position of axillary girth was at $RL_{0.38} \pm 0.04$.

Blubber was thickest in both females and males dorsally at $RL_{0.5}$, but most variable at $RL_{0.4}$ ($n=47$, Tables 3,4). Variance did not differ significantly, however, from $RL_{0.4}$ to $RL_{0.5}$ or $RL_{0.6}$ for females ($F_{20,20}=1.16$, $p>0.05$ and $F_{20,20}=1.38$, $p>0.05$, respectively) or males ($F_{25,25}=1.11$, $p>0.05$ and $F_{25,25}=1.19$, $p>0.05$, respectively). Generally, blubber was most variable dorsally and least variable ventrally. Variance was greater in females than males dorsally from $RL_{0.3}$ to $RL_{0.8}$ and laterally and ventrally between $RL_{0.5}$ and $RL_{0.7}$. In both sexes, blubber thickness was significantly more variable dorsally at $RL_{0.5}$ than at the ventral position $RL_{0.4}$ which corresponds to the more commonly measured sternal blubber thickness (females $F_{20,20}=5.24$, $p<0.001$; males $F_{25,25}=4.66$, $p<0.001$).

Xiphosternal blubber thickness, measured before sculping, did not differ significantly from blubber thickness at the equivalent post-sculping, interpolated ventral position at $RL_{0.4}$ ($t=0.49$, $df=50$, $p>0.05$). However, comparison of sculp width to the corresponding interpolated girths prior to sculping showed significant shrinkage had occurred ($t=-37.7$, $df=344$, $p<0.0001$). In absolute terms, shrinkage varied with RL ($F_{6,338}=12.32$, $p<0.0001$) and was greatest in the range $RL_{0.3}$ to $RL_{0.7}$. When expressed as a percent, however, no significant bias in shrinkage

was observed between the different reference lengths ($F_{6,338}=1.33$, $p>0.05$). Mean shrinkage of the sculp, across the width, was $17.5\% \pm 5.3$ (mean $\pm$ 1sd).

Blubber did not vary significantly in lipid content among the 5 body sites ($F_{4,20}=0.67$, $p>0.05$) and 3 depths sampled ($F_{2,50}=1.42$, $p>0.05$). Body site and blubber depth did not interact to affect lipid content ($F_{8,50}=1.25$, $p>0.05$). Individuals varied significantly in blubber lipid content when all sites and depths were combined for each ($F_{5,20}=7.72$, $p<0.001$). Lipid content in the 9 whole carcasses analyzed ranged from 38.5 to 49.6% of body mass. Body measurements and the lipid content of blubber, carcass, and viscera are presented (Table 5). Skin (with hair) from one specimen was 6.7% lipid by wet mass. Blubber, carcass, viscera and skin contributed 89.5 ± 1.5 , 8.7 ± 1.5 , 0.9 ± 0.3 , and 0.9% of total body lipid (mean $\pm$ 1sd). No significant adipose deposits were found associated with the viscera in any season.

The lipid content of hip and back muscle samples was not significantly different ($t=-0.49$, $df=74$, $p>0.05$). The values used for further analysis represent the average of the two muscles. Percent lipid in the carcass and muscle were correlated ($R^2=0.37$, $F_{1,7}=5.75$, $p<0.05$). The relationship is given by:

$$\text{Carcass lipid} = 3.54 \text{ Muscle lipid} + 3.79 \quad (s_{y \cdot x}=1.48)$$

where lipid content is expressed as a percent of wet tissue weight.

Correlations between body measurements and percent lipid of body mass and lipid mass adjusted for standard length³ were calculated (n=9, Table 6). Only sternal blubber thickness and sternal blubber thickness/length were significantly correlated to lipid content. Dorsal blubber thickness and girth/length indices showed stronger correlations to lipid mass adjusted for standard length³.

Blubber mass was measured directly for the specimens from Les Escoumins (n=50). All indices showed a stronger correlation to blubber mass/length³ than to percent blubber content (Table 7). Blubber thickness adjusted for standard length showed a stronger correlation to both percent blubber content and blubber mass/length³ than blubber thickness alone. Maximum girth/length showed the strongest correlation to blubber mass/length³, explaining 85% of the variation, whereas axillary girth/length accounted for only 67%. Blubber thickness showed the strongest relation to both indices when measured dorsally at RL_{0.5}.

Slopes of the following morphometric data as a function of standard length were found to be homogeneous for males and females in winter at Les Escoumins (ANCOVA, $p > 0.05$): total mass,

sculp mass, core mass, maximum girth, axillary girth, percent sculp mass of total mass, and blubber thickness at the sternum and dorsally at RL_{0.4}, RL_{0.5} and RL_{0.6}. The mean date of collection was not significantly different between the sexes ($t=0.229$, $df=33$, $p>0.05$, males 4 January $\pm$ 10.2, females 5 January $\pm$ 8.3, mean $\pm$ 1sd).

Compared by least-square means, both sexes showed seasonal differences in sculp and also core mass. Females, one month post-partum (April, Les Escoumins), had the greatest core mass, being significantly heavier than females collected at Salluit in the autumn ($t=2.84$, $df=14$, $p<0.01$, Table 8). Some of this increase is attributable to increased liver and intestine mass. Compared to winter females from Les Escoumins, animals in April had significantly heavier liver mass (2.1 ± 0.4 , 3.3 ± 0.3 kg, mean $\pm$ 1sd, respectively; $t=7.98$, $df=18$, $p<0.0001$). Intestine mass in females one month post-partum was greater than in winter by 3 kg ($t=7.15$, $n=20$, $p<0.0001$), but the seasonal difference in core mass was significant even when correction for fecal material in the intestine was made ($F_{3,22}=8.34$, $p<0.001$).

Males also showed significant variation in core mass. Those collected at Iles de la Madeleine were significantly heavier in 1990 than in 1989 ($t=-7.183$, $df=38$, $p<0.0001$). The difference results from heavier cores since mean sculp mass was slightly lighter in 1990 (Table 9). The high core mass of the 1990 sample

is reflected in the significantly larger axillary and maximum girths ($r=0.68$ and 0.61 , $p<0.0001$, respectively). The mean date of collection was significantly later in 1989 ($t=4.52$, $n=40$, $p<0.001$, 6 March ± 1.70 , mean $\pm 1sd$) than in 1990 (1 March ± 4.29).

Predictive equations were developed for percent blubber content (Table 10) and for blubber, sculp, core, skin and total body mass (Table 11). Standard length and axillary girth better predicted core and total body mass than did standard length and maximum girth. Blubber and sculp mass were best predicted by maximum girth and standard length. Skin mass was predicted well by standard length alone. Values predicted by the length-body mass-blubber thickness model of Ryg *et al.* (1990a) showed the strongest correlation to measured values of percent blubber content, accounting for 68% of the variation. When data on total body mass were not included in the model, percent blubber content was best predicted by the ratio of mean blubber thickness to girth at $RL_{0.5}$. Dorsal blubber thickness at $RL_{0.5}$ was more strongly correlated to percent blubber content than sternal blubber thickness. Girth/length indices were weakly correlated. If no direct measures of sculp or body mass are available, percent blubber content is better predicted by blubber thickness/girth at $RL_{0.5}$ than by separately calculating component masses (Table 12).

DISCUSSION

I observed sexual dimorphism with regard to length in mature harp seals, males being 3 cm (or 2.1%) longer than females, which is comparable to the findings of others (Khuzin 1963 (cited by Sergeant In press); Wiig 1989; Sergeant In press). Innes et al. (1981), however, found no difference between the sexes for any of the growth parameters they examined.

Harp seals have a pattern of blubber distribution slightly different from that observed by Ryg et al. (1988) in ringed seals, reflecting variation in shape between the two species. Ringed seal blubber is thickest and most variable dorsally at $RL_{0.6}$. Harp seal blubber, in contrast, is thickest dorsally at $RL_{0.5}$ and most variable dorsally between $RL_{0.4}$ and $RL_{0.6}$. Lockyer et al. (1985) and Ryg et al. (1988) suggest that blubber thickness at the most variable site is the preferred indicator of body condition. In the harp seal, I found that blubber thickness measured dorsally at $RL_{0.5}$ was consistently the best predictor of body fat.

Comparing various indices of condition in harbour seals, Pitcher (1986) found weak correlations of sternal blubber thickness to percent sculp mass ($r=0.56$, $n=413$, $p=0.001$) and to sculp mass/length ($r=0.690$, $n=407$, $p=0.001$). His sample included a large proportion of younger age classes and blubber thickness

was not standardized for body size. I believe that the weak correlation of condition indices, to which he refers, results more from the error associated with measuring blubber thickness at a site showing low variability and failure to correct for variation in body size, than in error of measuring sculp mass.

Whale blubber is a heterogeneous tissue, with lipid content showing considerable variation with both depth and body site (Ackman et al. 1975; Lockyer et al. 1984; 1985). Seal blubber, by contrast, lacks visible macroscopic heterogeneity (pers. observ.) and lipid has been considered to be homogeneously distributed (Jangaard and Ke 1968). Jangaard and Ke (1968) examined a single blubber sample from an adult female harp seal and found no difference in fatty acid composition between the outer, middle and inner depths. In the same study, blubber from 4 body sites in one 5-6 day-old hooded seal pup also showed no difference in composition. With a larger sample size, my study supports the theory that seal blubber is a homogeneous tissue, at least with respect to total lipid.

As with marine mammals in general, the greatest amount of body lipid in harp seals in my study was stored in the blubber (89.5%), with the carcass contributing most of the remaining lipid (8.7%). Estimates of nutritional condition in wintering harp seals, based on blubber lipid alone, underestimate the energy available from fat sources by about 10 percent. The

viscera were found to contribute very little toward the total lipid content of harp seals, and kidneys and other organs generally lacked additional fat deposits. This is in marked contrast to many terrestrial mammals which can have considerable fat deposits associated with internal organs. These internal fat depots have been used to estimate body condition in ungulates (Ransom 1965; Finger et al. 1981). The lack of visceral fat in Pinnipeds probably reflects preferential deposition of lipids in the blubber for insulation.

In order to compare body condition between the sexes or different age groups, it is essential that slopes for the regression coefficients be homogeneous. Murie (1984) rejected blubber thickness (measured over the sternum) as a potential index of condition because of heterogeneity of the regression coefficients (analysis of covariance, covariate=length), finding blubber thickness in mature males to decrease with length while increasing for juveniles and mature females. I did not observe this sexual difference in my sample collected in the same location and season. The small sample size and the potential error in measuring blubber thickness at this body site may have led to Murie's results. Other body measurements (body and component masses, girths and blubber thickness) did not display heterogeneity of slope between the sexes and could not be disregarded as potential indices of body condition on this basis.

The balance between core and blubber mass is important when considering thermoregulation in seals, since minimal heat loss can be maintained provided that changes in blubber mass are matched by parallel changes in core mass (Ryg et al. 1988). Generally, decreases in core mass have been associated with preferential maintenance of blubber for homeothermy in fasting or starving phocid seal pups (Stewart and Lavigne 1980; Oritsland et al. 1985; Worthy and Lavigne 1987). In contrast, seasonal mass fluctuations in mature animals have been attributed to variation in blubber and not core mass (Sergeant 1973; Stewart and Lavigne 1984; Ryg et al. 1990b). I found, however, that both blubber and core mass are subject to change on a seasonal and year-to-year basis.

Both sexes showed significant variation in body component masses. Among females, one month post-partum specimens collected in mid-April were heaviest. While sculp mass was lower in these females than in wintering animals at Les Escoumins from the same year, core mass was greater, significantly greater than the females from the arctic in October. In 1989, males were significantly heavier at Iles de la Madeleine than earlier winter samples collected in the St. Lawrence River estuary, resulting from heavier sculps. The difference in mass between the 1989 and 1990 samples collected at Iles de la Madeleine was due to heavier core mass in 1990. Since harp seals do not feed actively after arrival at the whelping ice (Sergeant 1973; In press), the later

mean collection date in 1989 could account for some of the observed mass difference. It seems unlikely, however, that the difference of 16 kg in core mass is attributable to 5 days difference in collection. Furthermore, it is questionable that core energy alone would be metabolized when large fat reserves in the blubber were present, especially considering the difference in the caloric content of protein and fats (Church and Pond 1974; Pike and Brown 1975).

The seasonal variation in core mass in harp seals may be related to a combination of factors including seasonal variation in feeding habits, costs of reproduction and the long annual migrations. While the high energy demand of lactation is known to deplete blubber stores, Stewart and Lavigne (1984) did not find a significant decrease in core mass in nursing females. There was, however, a general trend of decreasing core mass with increasing pup age, during lactation. Stewart (1983) calculated a loss of 0.7kg/day from the core of the lactating female, but the decrease was significant in 1982 alone ($p < 0.05$). The short duration of lactation in the harp seal makes it difficult to detect significant differences in core mass. Variation in feeding intensity and physical activity could also lead to significant seasonal changes in the mass of muscle and liver in mature animals. The heaviest core mass in females was observed in the one month post-partum specimens which had been feeding very intensively and which had the heaviest liver mass and also the

highest muscle and liver lipid content (see Chapter III). During the spring moult, harp seals spend much of the time hauled out on the ice and feed intermittently (Sergeant 1973). At this time, reduced core mass could be due to catabolism of proteins and energy stores in the liver as well as the atrophy of muscle tissue. Considerable energetic costs are associated with the northward migration and early summer season in the arctic. Harp seals swim against the Labrador current and feed on capelin which, in spring and summer, have a much lower caloric density than in autumn (Jangaard 1974). If blubber stores are sufficiently reduced, energy from the core may be mobilized to preferentially maintain blubber for thermoregulation. These factors would lead to an annual fluctuation in both blubber and core mass.

Percent blubber content is used to measure seasonal changes in body condition in seals and has been considered the standard to which other more easily obtained indices may be compared (Hammill 1987; Ryg et al. 1990a; 1990b). Interpretation of data has been based on the assumption that the seasonal fluctuations in mass of mature harp seal are related primarily to changes in blubber and not core mass (Sergeant 1973; Stewart and Lavigne 1984). The variation in core mass which I observed in both males and females would suggest that percent blubber content can produce misleading results, with respect to energy stores, when viewed in isolation. Females from the arctic had similar percent

blubber content to wintering animals, despite having significantly lower blubber mass. Males from Iles de la Madeleine in 1990 had significantly lower percent blubber content than in 1989, suggesting a state of lower nutritional condition, despite having about the same blubber mass.

Percent blubber content is important because it reflects how well insulated an individual animal is (Ryg et al. 1990a), however, harp seals may be exposed to water temperature as low as 0°C without increasing metabolic rate (Irving and Hart 1957). Gallivan and Ronald (1979) found that a harp seal with 33.3 percent blubber content was within its thermal neutral zone in water of 4°C. While heavy animals have higher metabolic rates (Kleiber 1975), they require proportionally less insulation due to the effects of scaling in surface area to volume ratios. Since harp seals undergo seasonal changes in core and total body mass, the proportion of fat necessary for homeostasis also undergoes some seasonal change, with lighter summer animals needing a higher percent blubber content than winter animals.

Considerable error is inherent in any measure and total body mass can vary from different sources. If the animal has been shot, blood loss prior to weighing can take place, the actual amount varying on the location of the shot and other factors. Since blood may represent 10 to 15% of total body mass (St. Aubin et al. 1978), the potential for error is great. Comparison of

mass or growth curves to detailed body measurements from live specimens should be made with caution. For the purpose of monitoring seasonal and sexual variation in component masses, correction should be made for the mass of stomach contents and foetus. A full-term foetus, which weighs up to 11 kg (Stewart and Lavigne 1980; Kovacs and Lavigne 1985), will significantly alter body mass.

For the purpose of monitoring seasonal changes in nutritional condition, blubber or sculp mass adjusted for body size (length^3) is more useful. In the nine specimens analyzed for total carcass lipid, maximum girth/length and mean blubber thickness/length (at $RL_{0.5}$) exhibited a strong correlation to total carcass lipid/length³, but were very weakly correlated to percent lipid of body mass. The same pattern was observed in the 50 samples for which blubber mass was measured directly. This indicates that these indices are more indicative of the energy stores than the state of thermal balance.

The stronger correlation of blubber thickness/length to percent blubber content and blubber mass/length³ versus blubber thickness alone indicates the importance of correcting for body size, even among a group of mature animals. The weaker correlation of axillary girth may reflect lack of sensitivity of traditional condition indices reported by McLaren and Smith (1985). Comparison of blubber mass or sculp mass by least-squares

(analysis of covariance) standardizes for variation in body size, provided slopes are homogeneous and adequate sample sizes for each group are available. This method was used for harp seals by Murie (1984) and has been recommended as an index of condition in fish (Cone 1989). The main source of error in this evaluation of condition is in the accurate measuring of length, but I believe error from this source to be less than that associated with total body mass and percent blubber content.

The best method to obtain blubber mass is obviously the direct one. However, it is usually too time-consuming and difficult under field conditions to carefully separate the skin from the blubber in order to obtain the separate component masses. Separation of the sculp from the carcass is usually part of the field procedure and can be done reasonably quickly and carefully with practice. Since skin mass can be predicted very well from length, blubber mass can be calculated by subtraction.

In the absence of direct measurements of mass, total body mass is best predicted from power functions based on axillary girth and length, and blubber and sculp mass from maximum girth and length. The site of maximum blubber thickness coincides with the position of maximum girth, so both predict blubber mass well. With an increased sample size, I believe that blubber thickness at $RL_{0.5}$ and length would yield a better predictive equation for blubber mass than girth and length since error in the girth

measurement associated with core diameter is eliminated. To avoid damaging the pelt, blubber thickness can be measured following removal of the sculp (as in the present study), but further study is needed to compare blubber thickness before and after removal of the sculp. Where desired, percent blubber content can be estimated from the ratio of blubber thickness to girth at $RL_{0.5}$. The mean of dorsal, ventral and lateral measures is preferable, but dorsal blubber thickness alone can be used.

Harp seals are lightest in summer following the northward migration (Sergeant In press), but also appear to have a lower relative percent blubber content since Inuit hunters report many animals sink when shot. Careful study during summer is needed to evaluate nutritional condition in this species.

Body condition indicates both the state of thermal balance and energy stores. Percent blubber content reflects the thermal balance and is most useful as an index of condition in harp seals for specimens from the arctic in summer, which may be near the lower limit of their thermal neutral zone. Variations in core mass may reflect the intensity of feeding and physical activity, but limit the value of percent blubber content as an index of seasonal and temporal changes. Since blubber is the largest store of energy in seals, blubber mass adjusted for length³ is the best index of energy reserves. By examining percent blubber content and the mass of both core and blubber, a more complete and

interesting evaluation of body condition is obtained. Comparison by least-square means standardizes for body size and is a useful method to evaluate indices of condition between different groups of animals.

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Table 1. Location and sampling date of all harp seal specimens examined for the evaluation of indices of nutritional condition.

Location	Sampling dates	Sample size					Total
		Males		Females			
		mature	immature	mature ¹	barren	immature	
Les Escoumins	20/12/88 - 27/02/89	26	0	12	3	0	41
Iles de la Madeleine	04/03/89 - 10/03/89	26	0	0	0	0	26
Les Escoumins	14/04/89 - 16/04/89	1	0	9	0	0	10
Salluit	02/09/89 - 04/10/89	2	1	8	0	0	11
Harrington Harbour	03/12/89 - 21/12/89	2	6	3	1	5	17
Iles de la Madeleine	25/02/90 - 08/03/90	14	0	0	0	0	14
Total		71	7	32	4	5	119

¹ includes pregnant and post-partum females

Table 2. Location and sampling date of mature specimens of harp seals compared for variation in body measurements with respect to season and location.

Location	Sampling dates	Males	Females
Les Escoumins	25/12/88 - 21/01/89	24	11
Iles de la Madeleine	04/03/89 - 08/03/89	23	-
Les Escoumins	14/04/89 - 16/04/89	(1)	9
Salluit	30/09/89 - 04/10/89	(1)	7
Iles de la Madeleine	25/02/90 - 10/03/90	17	-

() Excluded from tests of seasonal variation.

Table 3. Variance of blubber thicknesses associated with different body sites in all female harp seals collected at Les Escoumins (n=21), mean in parentheses (mm).

Reference length (RL)	Ventral	Left lateral	Dorsal	Right lateral
0.2	16.2 (36)	20.3 (32)	30.2 (32)	13.5 (33)
0.3	24.2 (46)	13.7 (37)	67.7 (47)	33.7 (38)
0.4	20.8 (46)	27.4 (46)	126.9 (60)	39.8 (47)
0.5	28.1 (46)	36.2 (49)	109.0 (65)	38.0 (50)
0.6	18.4 (45)	34.5 (50)	92.0 (64)	45.2 (51)
0.7	22.3 (44)	38.0 (49)	86.2 (59)	30.1 (50)
0.8	34.2 (47)	20.1 (47)	50.4 (45)	29.4 (47)

Table 4. Variance of blubber thicknesses associated with different body sites in all male harp seals collected at Les Escoumins (n=26), mean (mm) in parentheses.

Reference length (RL)	Ventral	Left lateral	Dorsal	Right lateral,
0.2	25.1 (34)	19.1 (31)	54.1 (29)	33.8 (31)
0.3	23.2 (45)	23.9 (37)	54.2 (43)	29.2 (36)
0.4	17.9 (44)	41.2 (45)	92.7 (56)	44.3 (45)
0.5	16.4 (44)	23.8 (47)	83.5 (60)	29.5 (47)
0.6	17.8 (44)	24.3 (48)	77.8 (59)	27.7 (47)
0.7	15.9 (46)	32.7 (47)	58.9 (54)	25.6 (47)
0.8	31.7 (44)	29.2 (44)	29.8 (40)	20.6 (43)

Table 5. Body measurements and lipid content of blubber, lean carcass, viscera and the whole carcass in harp seals from winter (Les Escoumins), expressed as percent of wet weight (n=9).

Specimen	Sex	Date	Age (years)	Length (cm)	Mass (kg)	Blubber	Lean carcass	Viscera	Whole carcass
PGE-88-21	F	12/27/88	10	168	136	97.2	11.5	6.9	45.1
PGE-89-25	F	01/07/89	10	160	103	97.6	7.1	3.7	41.2
PGE-89-33	F	02/15/89	7	167	124	97.9	14.1	5.3	46.2
PGE-88-24	M	12/27/88	7	159	111	94.5	9.7	5.9	39.4
PGE-89-37	M	01/03/89	8	161	110	97.4	6.5	3.8	41.2
PGE-89-40	M	01/03/89	3	154	81	96.3	8.2	8.2	41.1
PGE-89-41	M	01/07/89	7	176	105	98.8	8.8	8.8	44.2
PGE-89-22	M	01/10/89	6	162	98	98.2	9.2	9.2	47.9
PGE-89-35	M	02/27/89	16	161	111	96.9	7.2	7.2	38.5
Mean $\pm$ 1sd						97.2 $\pm$ 1.3	9.1 $\pm$ 2.4	5.1 $\pm$ 1.0	42.8 $\pm$ 3.2

Table 6. Correlation of indices of condition to total body lipid content and lipid mass adjusted for length in harp seals (n=9), Pearson Correlation Coefficients/(probability).

Condition Index	% Lipid of body mass	<u>Lipid mass</u> <u>Length³</u>
Blubber thickness (sternal)	0.8613 (0.0028)	0.7211 (0.0283)
<u>Blubber thickness (sternal)</u> length	0.7758 (0.0140)	0.7277 (0.2630)
Blubber thickness (dorsal) (at RL _{0.5})	0.5090 (0.1616)	0.8790 (0.0018)
<u>Blubber thick. (dors.RL_{0.5})</u> length	0.3309 (0.3844)	0.9022 (0.0009)
<u>Axillary girth</u> length	-0.0501 (0.8981)	0.7838 (0.0124)
<u>Maximum girth</u> length	0.1323 (0.7343)	0.8693 (0.0023)

Table 7. Correlation of indices of condition to percent blubber content and blubber mass adjusted for length in harp seals (n=50), Pearson Correlation Coefficients/(probability).

Condition Index	Blubber content (%)	<u>Blubber mass</u> Length ³
Blubber thickness (sternal)	0.5503 (0.0001)	0.5908 (0.0001)
<u>Blubber thickness (sternal)</u> length	0.5784 (0.0001)	0.6709 (0.0001)
Blubber thickness (dorsal) (at RL0.5)	0.7119 (0.0001)	0.7495 (0.0001)
<u>Blubber thick. (dors.RL0.5)</u> length	0.7553 (0.0001)	0.8630 (0.0001)
<u>Axillary girth</u> length	0.4374 (0.0013)	0.8200 (0.0001)
<u>Maximum girth</u> length	0.6030 (0.0001)	0.9236 (0.0001)

Table 8. Comparison of body measurements by least-square means between different locations and seasons in female harp seals, pregnant and post-partum (April), standard error in parentheses.

Variable	Salluit (autumn)	Les Escoumins (winter)	Les Escoumins (April)
Sample size	7	11	9
Length ¹ (cm)	160.1a (4.9)	163.5a (6.1)	167.9a (8.4)
Age ¹	18.1a (7.6)	10.4b (4.8)	16.3a (5.6)
Axillary girth (cm)	116.6a (2.27)	125.6b (1.73)	121.2ab (2.02)
Maximum girth (cm)	123.2a (2.24)	133.7b (1.71)	127.3a (2.00)
Blubber thickness (sternal, cm)	4.6a (0.35)	5.1a (0.26)	4.6a (0.31)
Blubber thickness (dorsal, RL _{0.6}) (cm)	5.5a (0.34)	6.8b (0.26)	6.0ab (0.30)
% sculp of mass ¹	51.4a (3.67)	50.3a (6.58)	44.0b (3.48)
Sculp mass (kg)	49.6a (2.66)	57.4b (1.87)	52.6ab (2.18)
Core mass (kg)	49.4a (3.54)	57.9ab (2.49)	64.9b (2.91)

¹ Compared by analysis of variance/ (standard deviation).
abc Non-significant differences in means with common letter ($\alpha=0.05$)

Table 9. Comparison of body measurements by least-square means between different locations and seasons in male harp seals, standard error in parentheses.

Variable	Les Escoumins (winter)	Iles Madeleine (1989)	Iles Madeleine (1990)
Sample size	24	23	17
Length ¹ (cm)	166.4a (7.9)	170.6a (6.7)	167.4a (5.8)
Age ¹	9.8a (5.2)	13.5a (5.8)	11.6a (4.3)
Axillary girth (cm)	124.3a (1.08)	126.7a (1.12)	130.2b (1.27)
Maximum girth (cm)	127.1a (1.09)	129.7ab (1.12)	133.1b (1.28)
Blubber thickness (sternal, cm)	4.3a (0.15)	5.7b (0.22)	5.5b (0.21)
% sculp of mass ¹	44.9a (3.51)	48.1b (2.70)	42.1c (2.24)
Sculp mass (kg)	52.0a (1.15)	59.2b (1.18)	57.6b (1.35)
Core mass (kg)	64.4a (1.35)	63.2a (1.40)	79.3b (1.59)

¹ Compared by analysis of variance/ (standard deviation).

abc Non-significant differences in means with common letter ($\alpha=0.05$)

Table 10. Regression equations to predict percent blubber content of harp seals from body measurements, in the form $y=mx+b$, mass in kg and all linear measurements in metres.

Independent variable	Slope (std err)	Intercept (std err)	R ²	df	F	prob>F
1. Ryg index ¹	3779.28 (371.89)	12.17 (2.81)	0.676	1,48	103.28	0.0001
2. <u>Mean BT</u> [§] girth	96.739 (11.565)	1.408 (4.627)	0.590	1,47	69.973	0.0001
3. Mean BT [§]	5.027 (0.638)	14.230 (3.293)	0.560	1,47	62.039	0.0001
4. Dorsal BT [§]	3.484 (0.496)	18.590 (3.147)	0.497	1,48	49.33	0.0001
5. <u>Dorsal BT</u> [§] girth	49.061 (7.320)	16.264 (3.564)	0.489	1,47	44.924	0.0001
6. <u>Max. girth</u> length	0.612 (0.116)	-7.372 (9.019)	0.3507	1,49	28.00	0.0001
7. Sternal BT	2.924 (0.634)	26.891 (2.958)	0.289	1,49	21.28	0.0001
8. <u>Ax. girth</u> length	0.477 (0.140)	4.646 (10.48)	0.175	1,49	11.59	0.0013

¹ Ryg index = $((\text{length}/\text{body mass})^{\frac{1}{2}}) \cdot (\text{BT}_{\text{dorsal}}^{\text{§}})$.

[§] Blubber thickness measured at RL_{0.5}.

Table 11. Power functions to predict blubber, sculp, skin, carcass and whole body mass of harp seals, linearized standard errors in parentheses, mass in kg and linear measurements in metres.

$$1. \text{ Blubber mass} = 20.5802 \cdot (\text{maximum girth})^{0.6488} \cdot (\text{length})^{0.3121} \\ (1.0667) \quad (1.1583) \quad (1.1886)$$

$$R^2=0.8770 \quad F=414.368 \quad df=2,114 \quad p<0.0001$$

$$2. \text{ Blubber mass} = 22.928 \cdot (\text{maximum girth})^{2.8450} \\ (1.025) \quad (1.1052)$$

$$R^2=0.8745 \quad F=209.54 \quad df=1,115 \quad p<0.0001$$

$$3. \text{ Blubber mass} = 1132.305 \cdot (\text{mean BT}^5)^{1.2213} \cdot (\text{length})^{0.8692} \\ (1.135) \quad (1.9847) \quad (1.2459)$$

$$R^2=0.8364 \quad F=123.69 \quad df=2,46 \quad p<0.0001$$

$$4. \text{ Blubber mass} = 21.8357 \cdot (\text{axillary girth})^{2.3672} \cdot (\text{length})^{0.4885} \\ (1.084) \quad (1.1860) \quad (1.2299)$$

$$R^2=0.8239 \quad F=272.297 \quad df=2,114 \quad p<0.0001$$

$$5. \text{ Blubber mass} = 340.065 \cdot (\text{dorsal BT}^5)^{0.8743} \cdot (\text{length})^{0.8751} \\ (1.258) \quad (1.070) \quad (1.283)$$

$$R^2=0.7834 \quad F=89.604 \quad df=2,47 \quad p<0.0001$$

$$6. \text{ Sculp mass} = 21.3425 \cdot (\text{maximum girth})^{2.3534} \cdot (\text{length})^{0.6515} \\ (1.0592) \quad (1.1397) \quad (1.1661)$$

$$R^2=0.8960 \quad F=500.759 \quad df=2,114 \quad p<0.0001$$

Table 11 (cont.)

7. Sculp mass	= 22.6129 . (axillary girth) ^{2.1245} . (length) ^{0.7892} (1.0732) (1.1608) (1.1983)
	R ² =0.8564 F=346.842 df=2,114 p<0.0001
8. Core mass	= 23.9409 . (axillary girth) ^{1.6039} . (length) ^{1.2139} (1.1070) (1.2395) (1.2975)
	R ² =0.7093 F=142.531 df=2,114 p<0.0001
9. Core mass	= 21.2831 . (maximum girth) ^{1.3974} . (length) ^{1.4395} (1.1094) (1.2665) (1.3200)
	R ² =0.6687 F=118.057 df=2,114 p<0.0001
10. Body mass	= 47.1720 . (axillary girth) ^{1.8643} . (length) ^{0.9905} (1.0508) (1.1102) (1.1353)
	R ² =0.9164 F=642.65 df=2,115 p<0.0001
11. Body mass	= 43.1421 . (maximum girth) ^{1.8680} . (length) ^{1.0410} (1.0521) (1.1222) (1.1454)
	R ² =0.9041 F=552.505 df=2,115 p<0.0001
12. Skin mass	= (length) ^{3.7363} (1.0405)
	R ² =0.9943 F=8838.14 df=1,50 p<0.0001

^s Blubber thickness measured at RL_{0.5}.

Table 12. Correlation of measured percent blubber content of harp seals to values predicted by regression equations.

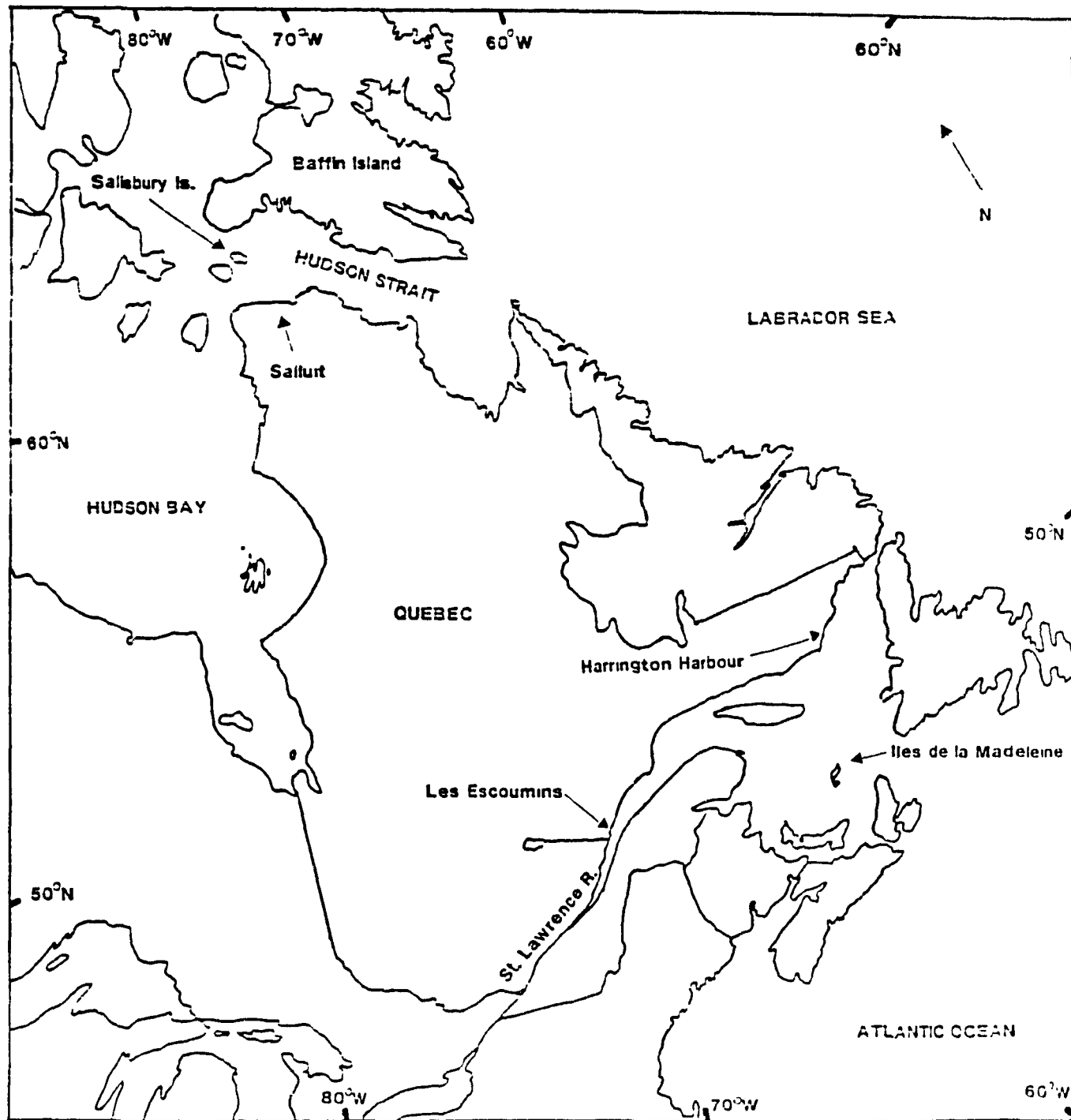
Method used to calculate blubber content	n	Pearson Correlation Coefficient	Probability
<u>Sculp mass¹ - skin mass (12)</u> body mass ¹	51	0.9882	0.0001
<u>Mean blubber thickness[§]</u> girth	49	0.7734	0.0001
<u>Dorsal blubber thickness[§]</u> girth	49	0.6991	0.0001
<u>Sculp mass(6) - skin mass (12)</u> body mass (10)	51	0.6295	0.0001

¹ Directly measured value.

[§] Blubber thickness to girth ratios at RL_{0.5}.

() Number of equation from Table 11 used to generate value.

Figure 1. Geographical location of communities in Quebec from which harp seal samples were obtained.



CONNECTING STATEMENT

In chapter II, I examined indices of nutritional condition based primarily on body measurements and established that variations in body component masses are the most accurate and direct means of monitoring condition. In Chapter III, seasonal variations in diet and feeding intensity are related to changes in body fat reserves and the lipid content in blubber, liver and muscle. Implications of seasonal feeding habits are discussed in relation to energy balance in the harp seal.

CHAPTER III

Seasonal variation in diet and nutritional condition of the
northwest Atlantic harp seal, Phoca greenlandica.

ABSTRACT

Harp seals Phoca groenlandica (n=124) obtained from hunters in Hudson Strait and the Gulf of St. Lawrence were examined for seasonal, sexual and age-specific variation in diet and nutritional condition. Date of collection ranged from December 1988 to October 1990. Condition was examined by two methods: (1) analysis of total lipid in muscle, liver and blubber and (2) variations in sculp (i.e. skin with attached blubber), core and total body mass. Harp seals on their southward migration fed less intensively than at other locations, but on a wider variety of fish and plankton. Capelin (Mallotus villosus) was the dominant prey of seals from the St. Lawrence River estuary in winter and spring and also in western Hudson Strait in autumn. The lipid content in blubber was slightly lower in immature seals than in mature animals ($97.0 \pm 1.9\%$ and $98.8 \pm 0.5\%$, respectively, $p < 0.05$), but muscle and liver lipid did not differ significantly. Pregnant females in autumn and winter maintained a higher lipid content in muscle and greater blubber mass than males. The lipid content of muscle and liver in both sexes was greater in winter than in autumn. Among females, those collected one month post-partum had the heaviest stomach content mass (mean=2.2kg) and the highest lipid content in muscle ($2.0 \pm 0.3\%$, mean $\pm$ 1sd) and liver ($7.3 \pm 1.4\%$). While these females had lower sculp mass than in winter and the lowest observed lipid content in blubber ($93.8 \pm 2.9\%$), the observed measurements were considerably higher than would be expected immediately following lactation. The relationship between prey selection, feeding intensity and nutritional condition is discussed.

INTRODUCTION

The Northwest Atlantic harp seal (Phoca groenlandica) undertakes long annual migrations, summering in the Canadian eastern arctic and wintering in Newfoundland and Gulf of St. Lawrence waters (Sergeant 1965). Seasonal variations in feeding habits and fat reserves have been observed and are intimately related to these migrations and to the annual events of parturition, mating and moulting (Sergeant 1973; Murie 1984; Stewart and Lavigne 1984).

Despite its status as the most abundant seal in the North Atlantic (Sergeant In press), few studies have examined seasonal variation in feeding habits of the harp seal (Bowen 1985). The work of Sergeant (1973; 1976; in press) provides the best overview. Other authors have examined diet in specific geographic locations (Dunbar 1949; Fisher and Mackenzie 1955; Myers 1959; Foy et al. 1981; Murie 1984; Lydersen et al. 1989; Wiig 1989). Recent studies have expanded the knowledge of feeding habits in the Canadian high arctic (Bradstreet et al. 1986; Kapel and Angantyr 1989; Finley et al. 1990).

The energetics of lactation and the early development of the pup have been studied intensively (Worthy and Lavigne 1983a; 1983b; 1987; Stewart and Lavigne 1984; Worthy 1987), but few

authors have examined seasonal and sexual variations in body condition. In general, harp seals are fattest in winter and leanest in summer following the northward migration (Sergeant 1973). Sternal blubber thickness and axillary girth/length have been used traditionally to evaluate variations in body condition, but the direct measurements of blubber or sculp mass (i.e. skin with blubber attached) adjusted for length are much more accurate (Chapter II; Read 1990), albeit slightly more labour intensive.

Study of seasonal changes in nutritional condition in the harp seal has been restricted to estimation of energy reserves in the blubber, although the importance of energy sources in the core has been suggested (Ryg et al. 1990). The lipid content of blubber and other tissues has been recorded in studies of contaminants (Addison et al. 1973; Frank et al. 1973; Jones et al. 1976; Ronald et al. 1984) and from an energetic perspective in post-natal pups (Worthy and Lavigne 1983a). Seasonal, sexual and age-specific variations in tissue lipids, however, have not been examined with respect to feeding and nutritional condition.

The potential conflict between harp seals and commercial fisheries and the general concern with pollutants in marine mammals has created a need for more detailed knowledge of this species. The study of contaminants is related to feeding patterns and the seasonal and sexual variations in fat reserves and is the subject of a concurrent study. Here, I examine diet in harp seals

from Hudson Strait and the Gulf of St. Lawrence and evaluate nutritional condition by analysis of lipid in blubber, liver and muscle tissue and by body measurements.

MATERIALS AND METHODS

Harp seals (n=124) were obtained from hunters at various sites in Quebec between December 1988 and October 1990 (Figure 1, Table 1). Specimens were taken by shooting at Les Escoumins (December 1988 to April 1989, n=51), Salluit-Hudson Strait (September to October 1989, n=11; October 1990, n=5) and Harrington Harbour (December 1989, n=17). Male specimens from Iles de la Madeleine were included in the analyses (late February/early March 1989, n=23, and 1990, n=17). Carcasses from Les Escoumins were frozen before being shipped to Montreal for dissection in the laboratory. All other specimens were processed in the field.

Carcasses were weighed whole and to the nearest kilogram, except for those over 90 kg taken at Harrington Harbour and Salluit (1989) where core and sculp were weighed separately. Specimens at Salluit were not weighed in 1990. Total body mass was corrected for the mass of stomach contents and foetus but not for blood loss. Standard measurements were made on all seals (American Society of Mammalogists 1967). Measurements of blubber thickness did not include the thickness of the skin. The sculp, not including flippers, was separated from the core and weighed. Blubber was separated from the skin and blubber mass determined by subtraction for specimens from Les Escoumins (n=51). Core mass was calculated as total body mass minus sculp mass. In the

laboratory, organs were weighed to the nearest gram (Sartorius Co., Model E5500S, Germany).

Age was determined by counting annular growth rings in the dentine of thin transverse sections of a lower canine tooth (Bowen et al. 1983). If by the third reading, 2 identical values were not obtained, results from the 3 readings were averaged. Reported age refers to age at the last anniversary, based on a mean parturition date in the Gulf of St. Lawrence of 2 March (Stewart et al. 1989). Ovaries were sectioned and examined to determine reproductive status. Females with at least one corpus luteum or corpus albicans present on the ovaries were considered sexually mature (Fisher 1954; McLaren 1958). Four of 36 sexually mature females obtained in 1988 and 1989 were barren and not included in the statistical analyses of seasonal variations in tissue lipid and body condition (ages: 8,16,23,31). Comparison of body condition between pregnant and barren females was not possible due to the limited sample size of the latter and variation in collection dates. Males which had attained a length of 152 cm were classified as mature (Laws 1956).

Sternal blubber, liver, hip and back muscle samples were analyzed for total lipid for 79 specimens. Lipid was extracted by micro-soxhlet refluxing for 4 hours with chloroform-methanol (2:1, by volume; Giese 1967; see Chapter II).

Stomachs collected in the laboratory (Les Escoumins winter and April) were preserved in 70% ethyl alcohol for one year, whereas those collected in the field were kept frozen until examined. Freezing is preferable since the quality of otoliths and other hard parts may deteriorate in alcohol (Recchia and Read 1989). Error may also be introduced in measurements of mass and volume of alcohol-preserved stomachs since contents must be drained. Stomachs were opened along the greater curvature, mass and volume measured and the proportion of fish and invertebrates of total stomach contents estimated by mass or visually if only trace amounts were present. Otoliths were retrieved by straining stomach contents through 1.0 and 0.5 mm sieves. Fish were identified primarily by examining the sagittal otoliths (Härkönen 1986), or infrequently by undigested fish material (Scott and Scott 1988). Staff and reference collections of Fisheries and Oceans Canada (Arctic Biological Station, Ste. Anne de Bellevue, Qc. and Institut Maurice Lamontagne, Mont Joli, Qc.) were helpful in identifying some otoliths and invertebrates.

Specimens were grouped by season and location (Table 2) to evaluate variation in tissue lipid content, percent fish in diet and the mass of stomach contents, organs, blubber and core. Statistical tests were performed using the Statistical Analysis System for personal computers (SAS Institute Inc. 1988, version 6.03). Mean values for body measurements and tissue lipid involving 2 groups were compared by t-tests, three or more means

by analysis of variance in GLM. Differences between 3 or more means were examined using Duncan's multiple range test (Proc GLM). When variances between 2 groups were not homogeneous, Proc t-test for unequal variance was used to evaluate the differences in means. In this case the sample size (n), rather than the adjusted df, is given in the results. Tests for normality were performed using Proc Univariate.

A single factor analysis of covariance (Proc GLM) was used to compare measurements which might be influenced by body size. Standard length was used as the single covariate for linear measurements and to maintain dimensional equality length cubed was used for mass (Stahl 1962). Homogeneity of slopes was established as a preliminary requirement for further analysis and comparison (Snedecor and Cochran 1967). The least-square option (ANCOVA) was used to calculate and evaluate differences between group means. Pearson Correlation coefficients were generated using Proc Corr.

Stomachs were defined as containing food if any prey item was found, including trace amounts and otoliths. Percent frequency of occurrence refers to the proportion of food-containing stomachs which contained a given prey item (Bigg and Perez 1985) and included all specimens from each location. Expected values were too low (Chi-square test, Zar 1984) to evaluate geographical and seasonal differences in prey species

groups (invertebrates, pelagic, ground and other fin fishes). The mass and percent fish in stomachs were compared (Proc Nparlway) between the following groups: 1989 and 1990 samples at Salluit, males and females at Les Escoumins (winter), mature and juveniles at Harrington Harbour and the seasonal/geographical groups (ages and sexes combined). Proc Nparlway uses tests comparable to Wilcoxon rank sum for 2 groups and the Kruskal-Wallis Chi-square approximation for 3 or more groups. Multiple comparisons were performed to locate differences between 3 or more groups (Daniel 1990).

Lipid content of muscle did not differ between the hip and back ($t=-0.49$, $df=74$, $p>0.05$), so tests were performed on the mean value of both body sites. Statistical comparisons of muscle and liver lipid were performed on the dry tissue values and on the wet tissue content for blubber.

RESULTS

More females than males were obtained at Salluit in both 1989 and 1990. With years combined, the difference in sex ratio was significant (females $n=13$, males $n=2$; $X^2=8.07$, $df=1$, $p<0.005$). Only 2 of 15 seals at Salluit were immature (1 female age=1; 1 male age=2).

I observed harp seals to feed on a variety of prey species, with the greatest number of fish species consumed by seals on their southward migration (Table 3). The relative importance of fish and plankton in individual stomachs varied significantly between locations (Kruskal-Wallis test, $X^2=16.686$, $df=3$, $p<0.001$). Seals at Harrington Harbour had a significantly greater proportion of plankton (notably Themisto libellula and Pandalus spp.) in their stomachs than at other locations (nonparametric multiple comparison, Daniel 1990, $p<0.05$; Table 4). The mass of stomach contents varied with season and location (Kruskal-Wallis test, $X^2=25.062$, $df=3$, $p<0.0001$) and was greatest in post-partum females at Les Escoumins (Table 4). Differences in stomach content mass and percent fish in diet were not observed between males and females at Les Escoumins (Wilcoxon 2-sample test, $Z=-0.526$, $n=24$, $p=0.599$ and $Z=0.290$, $df=24$, $p=0.772$, respectively,, between mature and juveniles at Harrington Harbour ($Z=0.159$, $df=12$, $p=0.873$ and $Z=0.167$, $df=11$, $p=0.867$) or between samples

collected at Salluit in 1989 and 1990 ($Z=0$, $df=12$, $p=0.999$ and $Z=0.581$, $df=11$, $p=0.561$).

Capelin (Mallotus villosus) was the dominant prey in winter and spring at Les Escoumins and at Salluit (98, 100 and 86% occurrence, respectively), both in frequency of occurrence and relative abundance within individual stomachs. At Salluit, arctic cod (Boreogadus saida) and crustacea (Themisto libellula and Mysidae) also occurred frequently, with 50 and 43% occurrence. The stomach from one mature male collected at north Salisbury Island (content mass=575 g) contained 60% plankton (Themisto libellula) and 40% fish (Boreogadus saida and Pleuronectidae). Large concentrations of harp seals, glaucous (Larus hyperboreus) and Iceland (Larus glaucoides) gulls were observed feeding pelagically at this location in August and September 1989. At Les Escoumins, redfish (Sebastes spp.) was the only fish prey other than capelin to occur in more than one stomach in winter or spring. Soft coral (Alcyonaria) occurred in 5 stomachs from winter at Les Escoumins, with 4 stomachs containing ≈ 350 g and the other ≈ 10 g. Sand lance (Ammodytes spp.) and Atlantic cod (Gadus morhua) were the most frequent food items at Harrington Harbour and occurred in 64 and 57% of the food containing stomachs. Bivalvia and Gastropoda occurred, but were small (less than 1 cm in diameter) and were probably ingested by prey fish.

Collectively, the 5 stomachs from Salluit (1990) contained otoliths from 246 capelin (114 in one stomach), 7 arctic cod, 1 rock cod (Gadus ogac), 1 flatfish (Pleuronectidae), and 1 sculpin (Cottidae). Trace quantities of mysids were found in 2 samples. None of the otoliths were retrieved from skulls. Atlantic cod otoliths found in seal stomachs at Harrington Harbour were small (otolith length = 6.3 ± 1.2 mm, $n=43$, mean $\pm$ sd), and correspond to a mean fish length of 14 cm (Harkonen 1986). One pair of large unidentified Gadidae otoliths not included in the calculations was found in one stomach (otolith length = 15 mm).

Muscle, liver and blubber were examined for sexual, age-specific and seasonal variations in lipid content. Pregnant female seals had higher muscle lipid content than males at all locations. This difference was significant in the winter group at Les Escoumins, the only site where sample size was large enough to permit statistical comparison between the sexes ($t=2.902$, $n=34$, $p<0.05$, Figure 2). Blubber and liver lipid content did not vary significantly between the sexes ($t=0.095$, $df=33$, $p>0.05$ and $t=-1.973$, $n=34$, $p>0.05$, respectively). I did not observe a difference in the lipid content of any tissue between the sexes ($p>0.05$) in juvenile or mature seals at Harrington Harbour ($p>0.05$), but the power of the tests were small due to the limited sample size. The sexes were grouped for comparison of age classes. Mature specimens at Harrington Harbour had significantly higher blubber lipid content than juveniles, but the difference

was small ($t=-2.763$, $n=15$, $p<0.05$, Table 5). Differences between the two age groups were not observed in muscle or liver lipid content ($t=-0.943$, $df=13$, $p>0.05$ and $t=0.600$, $df=13$, $p>0.05$, respectively).

Mature male and pregnant female harp seals showed similar seasonal trends in the lipid content of muscle and liver. The small sample size from some locations, however, limited statistical comparison to the 3 groups of females only (Salluit and Les Escoumins in both winter and April). In both sexes, lipid in muscle was higher at Harrington Harbour and Les Escoumins in winter than at Salluit in an autumn sample. Among females, the lipid content of muscle differed significantly with season and location, ($F_{2,24}=5.73$, $p<0.01$, Figure 2). Liver lipid also varied with season for females ($F_{2,24}=6.75$, $p<0.01$, Figure 3). The lipid content of liver was lowest in both sexes at Harrington Harbour during the southward migration. The highest observed lipid content in muscle and liver was in post-partum females. With all specimens considered, the lipid content of liver and muscle were weakly correlated (wet tissue: $r=0.399$, $n=76$, $p<0.001$; dry tissue: $r=0.304$, $n=76$, $p<0.01$). Post-partum specimens had the lowest lipid content in blubber, significantly lower than females collected at the same location in winter ($t=-2.958$, $n=20$, $p<0.05$, Figure 4).

Water content did not vary significantly between the 3 groups of females for either muscle ($F_{2,24}=1.61$, $p>0.05$) or liver ($F_{2,24}=2.45$, $p>0.05$). The range of water content among all groups was quite narrow (muscle: 68.2-71.3%, liver: 63.1-68.1%), with the highest values at Harrington Harbour. The water content of muscle was greater than that of liver ($69.1 \pm 1.4\%$ and $65.5 \pm 2.1\%$, respectively, mean $\pm$ sd).

Differences in the overall fat reserves were observed between male and female seals from Les Escoumins in winter. Pregnant females had slightly greater total body mass than males and significantly greater sculp mass and blubber content ($t=3.57$, $df=34$, $p<0.01$; $t=3.44$, $df=34$, $p<0.001$; Table 6). Blubber thickness measured dorsally, 50% of length posterior to the snout, and over the sternum were significantly thicker in the females ($t=2.66$, $df=34$, $p<0.05$ and $t=2.43$, $df=34$, $p=0.021$, respectively). Axillary girth, adjusted for the covariate length, did not show a significant difference between the sexes ($t=1.71$, $df=34$, $p=0.096$) whereas maximum girth did ($t=4.09$, $df=34$, $p=0.0003$).

Seasonal variation in total body mass was observed in both sexes (Figure 5,6), reflecting significant changes in the mass of core and sculp (Chapter II). The parallel increase in core and sculp mass in females from autumn to winter resulted in little variation in percent blubber content (Figure 7). Core mass was

lower in males collected at Salluit and Harrington Harbour than those from winter, but sample size was too small for statistical comparison. Sculp mass in males increased significantly from early to late winter (Chapter II) and is reflected in the increased percent sculp mass ($t=-3.60$, $df=45$, $p<0.001$, Figures 5,6). Maximum girth/length showed a small, but insignificant, increase during the winter ($t=-0.85$, $df=45$, $p>0.05$). Due to limited sample size, comparison of early and late winter measurements was not possible for females.

DISCUSSION

At some locations, segregation of harp seals by sex and age classes occurs. In summer, adults go farther north and into Hudson Bay whereas juveniles are more frequent on the west Greenland coast (Sergeant 1965). Along the Labrador coast, juveniles are more frequent at offshore islands and infrequently enter bays where adults feed heavily (Foy et al. 1981). In the high arctic, Finley et al. (1990) observed a greater number of males than females. At Salluit in October 1989 and 1990, 10 females and only 2 males were taken in or near the mouth of the fjord. Although sample size is small, the difference is significant and suggests sexual segregation occurs at this location and season. Only 2 seals at Salluit were immature, indicating segregation by age occurs in this region also.

The study of diet in marine mammals is of interest because it reflects the relationship between different trophic levels in the marine environment (reviewed in Lavigne et al. 1982; McLaren and Smith 1985) and because it helps evaluate potential conflicts with commercial fisheries (Lavigne 1982; Beverton 1985; Bowen 1985; Harwood and Croxall 1988; Wing 1989). Frequently, discussion of competition between seals and the fishing industry proceeds without reference to the particular species concerned, population sizes or the seasonal variations in abundance and feeding habits. Being the most numerous Pinniped in Canadian

Atlantic waters, the harp seal is frequently at the centre of such controversy.

The wide range of prey species consumed at Harrington Harbour reflects the opportunistic feeding habits of the harp seal. In certain locations and seasons, however, harp seals are known to specialize on particular prey types. My study confirms that capelin is the preferred food of harp seals not just in the St. Lawrence River estuary as has been previously described (Sergeant 1973; Murie 1984), but also in Hudson Strait. Dunbar (1970) described capelin in Hudson and Ungava Bays as isolated, relic populations which entered these northern waters during a warmer climatic period. Capelin is now described as having a continuous distribution from Hudson Bay to Nova Scotia (Scott and Scott 1988) and its frequent occurrence in harp seal stomachs at Salluit indicates its abundance at that location. Both arctic cod and capelin are present at Salluit, but the latter was the chief prey and was being fed upon heavily. Gaston and Noble (1985) found that thick-billed murre (Uria lomvia) near Digges Island (150 km west of Salluit) fed on capelin, but lance and arctic cod were the more frequent fish prey. The large concentrations of harp seals, glaucous and Iceland gulls observed feeding on plankton at north Salisbury Island may have been eating Themisto libellula, which was found in the stomach of the one male collected at this location. In some locations, crustacea forms the main prey of harp seals (Smith et al. 1979; Lydersen et al. 1989), despite often having a lower caloric content than capelin

(Jangaard 1974; Percy and Fife 1981; Murie 1984) and having low energy assimilation rates relative to fish (Keiver et al. 1984).

At Harrington Harbour, diet was varied but lance occurred most frequently. Being a small, schooling fish it is similar in habits to capelin and may occur in the diet of harp seals more frequently than is recorded in the literature. Foy et al. (1981), observed harp seals on the Labrador coast to feed primarily on capelin in bays and on sand lance at offshore islands. My results from the Quebec Lower North Shore and Hudson Strait suggest a similar pattern: sand lance was the most frequent item in stomachs collected at offshore islands (Harrington Harbour), whereas capelin dominated in stomachs collected at Salluit (within or near the mouth of the fjord). The frequent occurrence of sand lance in harp seal stomachs at Harrington Harbour may also coincide with a period of local abundance of this species.

I observed more frequent feeding in migrating harp seals than Sergeant (1973). Of the 16 stomachs I examined from Harrington Harbour, 14 contained food, but only 5 had contents weighing over 50 g. In the previous study, trace amounts of food in stomachs may not have been considered. Atlantic cod was found in the stomachs of harp seals from this location, but the number of fish consumed by all specimens combined was quite low (n=24).

Various methods have been used to estimate relative importance of prey items in the diet of seals (reviewed in Bigg

and Perez 1985). The retrieval of sagittal otoliths from the stomach, intestine and scats of marine mammals provides a useful means to identify the fish species consumed (Fitch and Brownell 1968; Treacy and Crawford 1981; Benoit 1989; Recchia and Read 1989). The method described by Murie and Lavigne (1986; Murie 1984), based on the number of stomach retrieved otoliths remaining within skull cases, provides a means to calculate daily fish consumption. While a reduction in the quality and quantity of otoliths has been observed to accompany digestion (da Silva and Neilson 1985), I found most otoliths retrieved in stomachs to be in good condition and readily identifiable. None of the otoliths from seals at Salluit were found within skull cases and therefore the large number of otoliths seen reflects only a fraction of the fish consumed.

The seasonal and interspecific variation in caloric density of prey species, together with availability, may be the proximate reason for changes in the diet and feeding intensity of harp seals. Murie (1984) observed capelin in the St. Lawrence river estuary in winter to have twice the caloric density (2.4 kcal/g) of any other fish or crustacea she examined. In the Northeast Atlantic, Wiig (1989) reported capelin to have a caloric density of 1.5-2.4 kcal/g and arctic cod 1.0 kcal/g, however the season of collection was not specified. The fat content of capelin may be as low as 2% following spawning in early summer, but increases rapidly to as much as 20% by late autumn before beginning to decline steadily through winter and spring (Jangaard 1974). In

summer, arctic cod is a rich source of energy and is preyed upon heavily by harp seals in the high arctic (Kapel and Angantyr 1989; Finley et al. 1990). At Salluit, I observed seals to specialize on capelin which in October is very fat rich. Harp seals feeding on fish in April must double the amount eaten in early winter to compensate for the variation in capelin fat stores and to maintain the same caloric intake. This, combined with reduced energy stores following lactation, may explain why the heaviest observed stomach mass was in the April sample.

The increasing muscle lipid content and blubber and core mass from autumn to early winter indicate that metabolic costs associated with the southward migration are low and perhaps assisted by the high seasonal fat content of prey and the flow of the Labrador Current. While harp seals appear to arrive in the estuary of the St. Lawrence in relatively good condition, males were observed to further increase their fat reserves over the course of the winter. A late winter sample of females was not available. The winter and early spring feeding period is of great importance because adequate fat reserves must be stored to last through the moult when feeding is intermittent and also for the ensuing northward migration. The lipid content of capelin and plankton in the arctic in early summer is low (Jangvard 1974; Lee 1975; Percy and Fife 1981) and the reduced caloric intake could adversely affect survival in animals which lacked adequate fat reserves stored before the northward migration.

Variations in the lipid content and mass of liver appear to reflect short-term changes in nutritional condition. The liver serves as a storage organ for glycogen and lipid, but is also the path by which fats are deposited or retrieved from adipose tissue (Pike and Brown 1975; Hamilton and Whitney 1982; Hoar 1983). The decreased liver lipid content of migrating seals at Harrington Harbour probably indicates that lipids from the liver are mobilized during migration. The high lipid content and mass of liver in post-partum females could reflect both an increase in stored lipid in the liver and also lipids being transported to the blubber. The mass of liver as an indicator of relatively rapid changes in nutritional condition should be examined carefully.

Pregnant females had significantly greater blubber mass than males in winter at Les Escoumins. The difference of 8 kg in the blubber is reflected in the greater maximum and axillary girths observed in the females. Females also maintained higher lipid content in muscle than males throughout the autumn and winter. In humans and in other animals, the higher levels of body fat in females have been related to the energetic costs of pregnancy and lactation (Frisch 1990). In harp seals, the period of lactation lasts about 12 days (Kovacs and Lavigne 1985), but owing to the high fat content of the milk (29-50% lipid, Sivertsen 1941; Cook and Baker 1969; Stewart *et al.* 1983), the transfer of energy to the pup is considerable (Lavigne *et al.* 1982; Stewart and Lavigne 1984).

Post-partum females while having the highest liver and muscle lipid had the lowest observed blubber lipid content. Because of the high fat content of the milk in harp seals, the cost of lactation may reduce both the mass and the lipid content of the blubber. Published values for the blubber lipid content of females on the breeding grounds vary from as low as 75.3% lipid (Ronald et al. 1984) to 99.8% (Frank et al. 1973). Frank et al. (1973) observed the highest lipid content in blubber, but at least some of their samples were collected before the start of the commercial hunt, and presumably before or early in lactation. Females in my sample had significantly reduced blubber lipid one month after weaning and I suspect that this difference would be even greater immediately following lactation. Reduction in the lipid content of blubber may also occur in males during the spring moult. Variation in the mass as well as lipid content of blubber has implications for the evaluation of contaminant burdens in marine mammals.

By mid-April, post-partum animals appear to have replenished a considerable portion of the body fat lost during lactation. Stewart and Lavigne (1984) calculated sculp mass to decrease by 24 kg during lactation. In my sample from Les Escoumins, post-partum females had a sculp mass of 53 kg, 14 kg heavier than that estimated by Stewart and Lavigne (1984) for females at the end of lactation, and not significantly lower than the sculp mass of females in my sample from earlier in the winter. This rapid

increase in body fats is impressive, particularly when the reduced lipid content of capelin in April is considered. It is unclear whether this is indicative of trends throughout the range of the harp seal or just a reflection of the great local abundance of capelin in the St. Lawrence River estuary.

Inuit hunters report that harp seals shot in summer usually sink, reflecting low body fat content. The reduction in blubber mass appears to be coincidental with a reduction in core mass. Fat reserves in summer may be so depleted following the northward migration that blubber is retained preferentially for insulation, as has been observed in fasting and starving phocid seal pups (Oritsland et al. 1985; Worthy and Lavigne 1987). Core mass may also be lost during the moult in spring when seals feed intermittently and rest on ice (see Chapter II). The low muscle lipid content and body mass observed in male and females from the arctic in autumn indicates that the replenishment of energy stores in the arctic following the spring moult and northward migration is a slow process.

The northward migration appears to be energetically costly for harp seals, and consequently its value to the species may be questioned. Finley et al. (1990) suggest that the high energy content of arctic cod relative to capelin in summer may be the proximate reason for the long migrations. Sergeant (1973) argues that harp seals require both an abundant pelagic food supply and their preferred resting substrate, pack ice, both of which are

present in many parts of the arctic throughout the summer. In addition, Sergeant (1973) suggests that the northward migration may reduce interspecific competition with whale species which also feed on capelin in the St. Lawrence River estuary, but during the summer months.

With an increasing harp seal population (Roff and Bowen 1983; 1986) and a decline in many commercial fish populations, reduced body condition in seals might be expected. Comparison to earlier studies, however, is inconclusive. In winter specimens from the St. Lawrence River estuary, sternal blubber thickness was 1 cm greater in Sergeant's (1973) study than my own. Compared by axillary girth/length, females were in slightly better condition in Sergeant's study, but males showed no difference. The estimate of female condition at the start of lactation by Stewart and Lavigne (1984; all years combined) was no different from my data in early winter when compared by axillary girth/length. Pre-lactation females had a predicted sculp mass 6 kg heavier than early winter females. If further fattening occurs during the winter (as observed in males in 1989), I do not believe that a difference in body condition exists between the present study and that of Stewart and Lavigne (1984). I found sternal blubber thickness and axillary girth/length to be poorly correlated to fat reserves (see Chapter II), so comparison by these indices may be inappropriate due their insensitivity.

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Table 1. Location and sampling date of all harp seal specimens examined for variation in diet and nutritional condition.

Location	Sampling dates	Sample size					Total
		Males		Females			
		mature	immature	mature ¹	barren	immature	
Les Escoumins	20/12/88 - 27/02/89	26	0	12	3	0	41
Iles de la Madeleine	04/03/89 - 10/03/89	26	0	0	0	0	26
Les Escoumins	14/04/89 - 16/04/89	1	0	9	0	0	10
Salluit	02/09/89 - 04/10/89	2	1	8	0	0	11
Harrington Harbour	03/12/89 - 21/12/89	2	6	3	1	5	17
Iles de la Madeleine	25/02/90 - 08/03/90	14	0	0	0	0	14
Salluit ²	13/10/90 - 20/10/90	0	0	3	1	1	5
Total		71	7	35	5	6	124

¹ Pregnant or post partum females.

² Includes 2 specimens for which only stomach and jaw available.

Table 2. Location and sampling date of mature specimens of harp seals compared for variation in body measurements with respect to season and location.

Location	Sampling dates	Males	Females
Les Escoumins	25/12/88 - 21/01/89	24	11
Iles de la Madeleine	04/03/89 - 08/03/89	23	-
Les Escoumins	14/04/89 - 16/04/89	(1)	9
Salluit	30/09/89 - 04/10/89	(1)	7
Iles de la Madeleine	25/02/90 - 10/03/90	17	-

() Excluded from tests of seasonal variation.

Table 3. Number of occurrences and percent frequency of occurrence (in parentheses) of prey items in food containing stomachs of harp seals.

Prey	Salluit (October)	Harrington Harbour (December)	Les Escoumins (winter)	Les Escoumins (April)	Total (n=78)
Teleostei	14 (100)	13 (93)	41 (100)	9 (100)	77 (99)
Capelin <u>Mallotus villosus</u>	12 (86)	2 (14)	40 (98)	9 (100)	63 (81)
Sand lance <u>Ammodytes</u> spp.	1 (7)	9 (64)			10 (13)
Atlantic cod <u>Gadus morhua</u>		8 (57)			8 (10)
Flatfish <u>Pleuronectidae</u>	3 (21)	5 (36)			8 (10)
Arctic cod <u>Boreogadus saida</u>	7 (50)				7 (9)
Redfish <u>Sebastes</u> spp.			6 (15)		6 (8)
Rock cod <u>Gadus morhua</u>	2 (14)	1 (7)			3 (4)
Rock gunnel <u>Pholis gunnellus</u>		3 (21)			3 (4)
Atlantic herring <u>Clupea harengus</u>		2 (14)			2 (3)
Sculpin <u>Cottidae</u>	1 (7)	3 (21)			4 (6)
Alewife <u>Clupea harengus</u>		1 (7)			1 (1)
Atlantic tomcod <u>Microgadus tomcod</u>		1 (7)			1 (1)
Rainbow smelt <u>Osmerus mordax</u>			1 (2)		1 (1)
Atlantic salmon <u>Salmo salar</u>				1 (9)	1 (1)

Table 3. (cont.)

Prey	Salluit (October)	Harrington Harbour (December)	Les Escoumins (winter)	Les Escoumins (April)	Total (n=78)
Invertebrata	6 (43)	12 (86)	9 (22)	0 (0)	27 (35)
Crustacea	6 (43)	12 (86)	7 (17)		25 (32)
<u>Themisto libellula</u>	4 (29)	12 (86)			16 (21)
Mysidae	3 (21)				3 (3)
<u>Pandalus</u> spp.		7 (50)			7 (9)
Unidentified		5 (36)	5 (12)		12 (15)
Alcyonaria			5 (12)		5 (6)
Gastropoda		1 (6)			1 (1)
Bivalvia		1 (6)			1 (1)
Stones	2 (14)		1 (2)		3 (4)
Food containing stomachs	n=14	n=14	n=41	n=9	n=78
Empty stomachs	n=2	n=2	n=0	n=1	n=5
Total number stomachs examined	n=16	n=16	n=41	n=10	n=73

Table 4. Comparison of mass of contents (kg) of food containing stomachs in harp seals, % fish/invertebrates in parentheses. Multiple comparison procedure based on mean rank for each sample $\alpha=0.05$ (Daniel 1990).

	Salluit (n=13)	Harrington Harbour (n=13)	Les Escoumins (winter) (n=25)	Les Escoumins (April) (n=8)
Mean	0.51 (91/9)	0.19 (80/20)	0.27 (86/14)	2.62 (100/0)
Range	T ¹ - 1.50 (40/60-100/0)	T - 0.90 (0/100-100/0)	T - 0.85 (10/90-100/0)	1.51-4.33 (100/0-100/0)
Median ²	0.27a (100/0ab)	T a (90/10a)	0.12a (100/0ab)	2.08b (100/0b)

¹ T=trace amount < 10g.

² Common letters represent non-significant differences at $\alpha=0.05$.

Table 5. Comparison of the percent lipid content in muscle, liver and blubber between mature and juvenile harp seals at Harrington Harbour, December 1989. Expressed as percent lipid of wet tissue weight, percent lipid of dry tissue weight in parentheses (mean $\pm$ sd).

Tissue	Juvenile ¹	Mature ²	Significance Level ³
Muscle	1.5 $\pm$ 0.3 (5.0 $\pm$ 0.8)	1.6 $\pm$ 0.3 (5.5 $\pm$ 1.0)	NS
Liver	4.9 $\pm$ 0.6 (14.3 $\pm$ 1.4)	4.8 $\pm$ 1.3 (13.7 $\pm$ 3.0)	NS
Blubber	97.0 $\pm$ 1.9	98.8 $\pm$ 0.5	*

¹ Males n=6, females n=4.

² Males n=2, females n=3.

³ NS - no significant difference in means at $\alpha=0.05$

* - significant difference in means at $\alpha=0.05$

Table 6. Comparison of body measurements by least-square means between male and female harp seals in early winter in the St. Lawrence River estuary.

Variable	Males (n=24)	Females (n=11)	Significance Level [§]
Body mass (kg)	112.3 ± 2.3	118.0 ± 3.4	NS
Sculp mass (kg)	50.4 ± 1.3	58.5 ± 1.9	**
Core mass (kg)	61.9 ± 1.8	59.5 ± 2.6	NS
Percent blubber content	38.9 ± 0.9	44.8 ± 1.4	**
Axillary girth (cm)	122.9 ± 1.2	126.6 ± 1.8	NS
Maximum girth (cm)	125.8 ± 1.2	134.6 ± 1.8	**
BT _{0.5} ¹ (cm)	6.0 ± 0.2	6.9 ± 0.3	*
BT _{sternum} ² (cm)	4.3 ± 0.2	5.1 ± 0.3	*
Length (cm)	166.4 ± 7.9	163.5 ± 6.1	NS
Age (years)	9.8 ± 5.2	10.4 ± 4.8	NS
Date	04JAN89±10.2	05JAN89±8.3	NS

§ NS - no significant difference in means at $\alpha=0.05$.

* - significant difference in means at $\alpha=0.05$.

** - significant difference in means at $\alpha=0.01$.

¹ Blubber thickness measured dorsally at 50% of length.

² Blubber thickness measured over the sternum.

Figure 1. Geographical location of communities in Quebec from which harp seal samples were obtained.

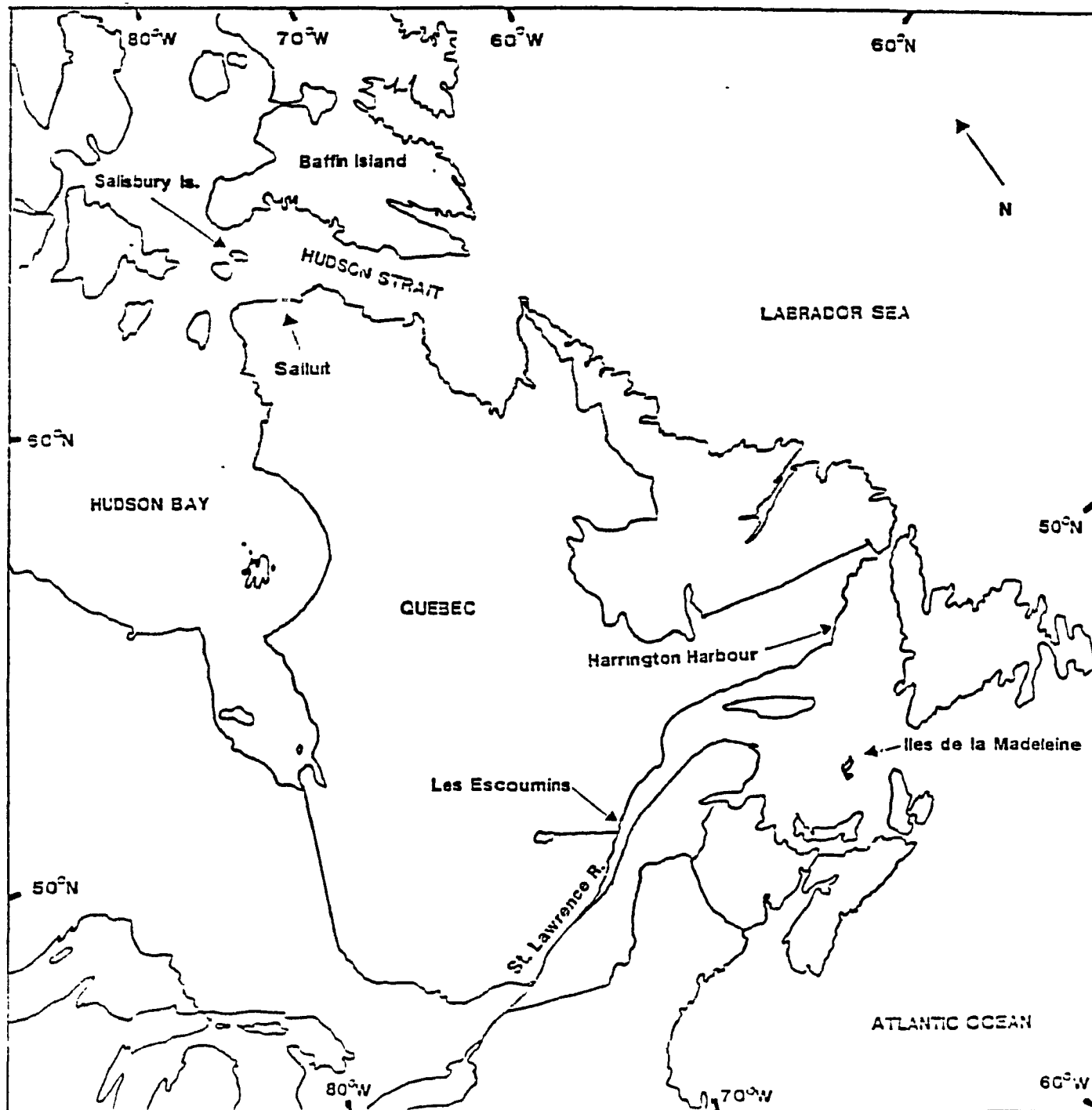


Figure 2. Seasonal and sexual variation in the lipid content of muscle tissue in harp seals. Means $\pm$ 1sd, sample size (n); common subscripts represent non-significant differences in means ($\alpha=0.05$).

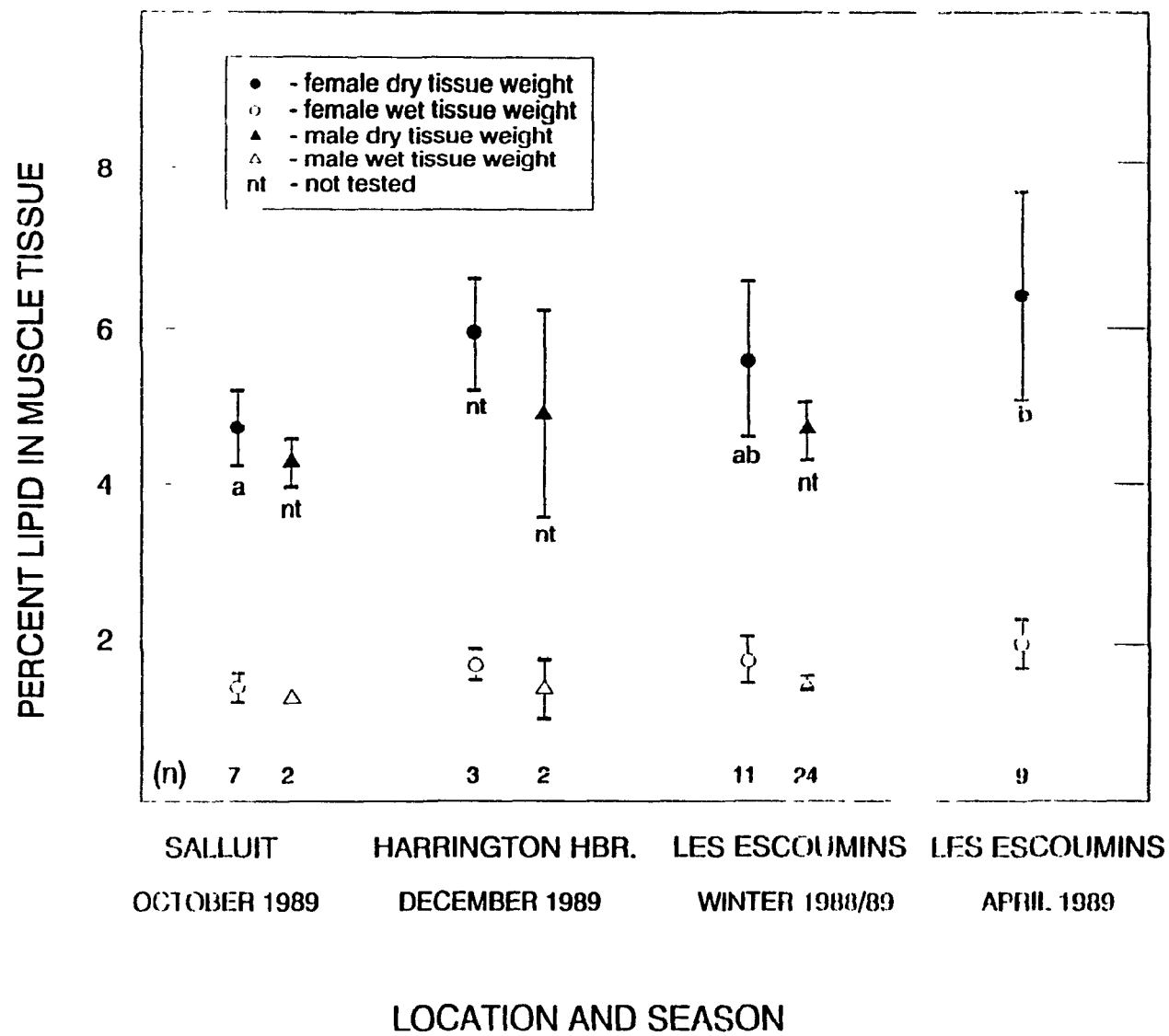


Figure 3. Seasonal and sexual variation in the lipid content of liver tissue in harp seals. Means $\pm$ lsd, sample size (n); common subscripts represent non-significant differences in means ($\alpha=0.05$).

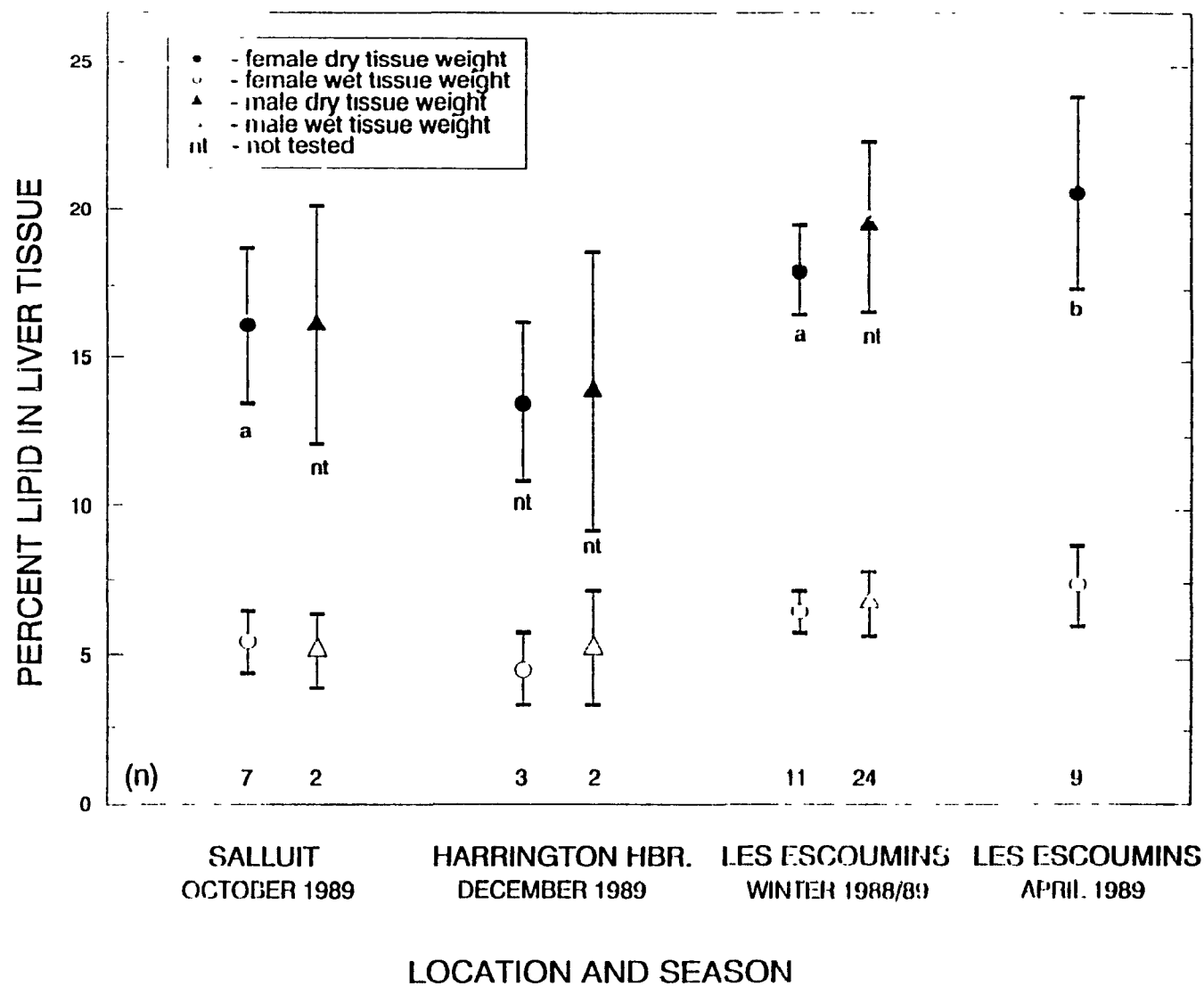
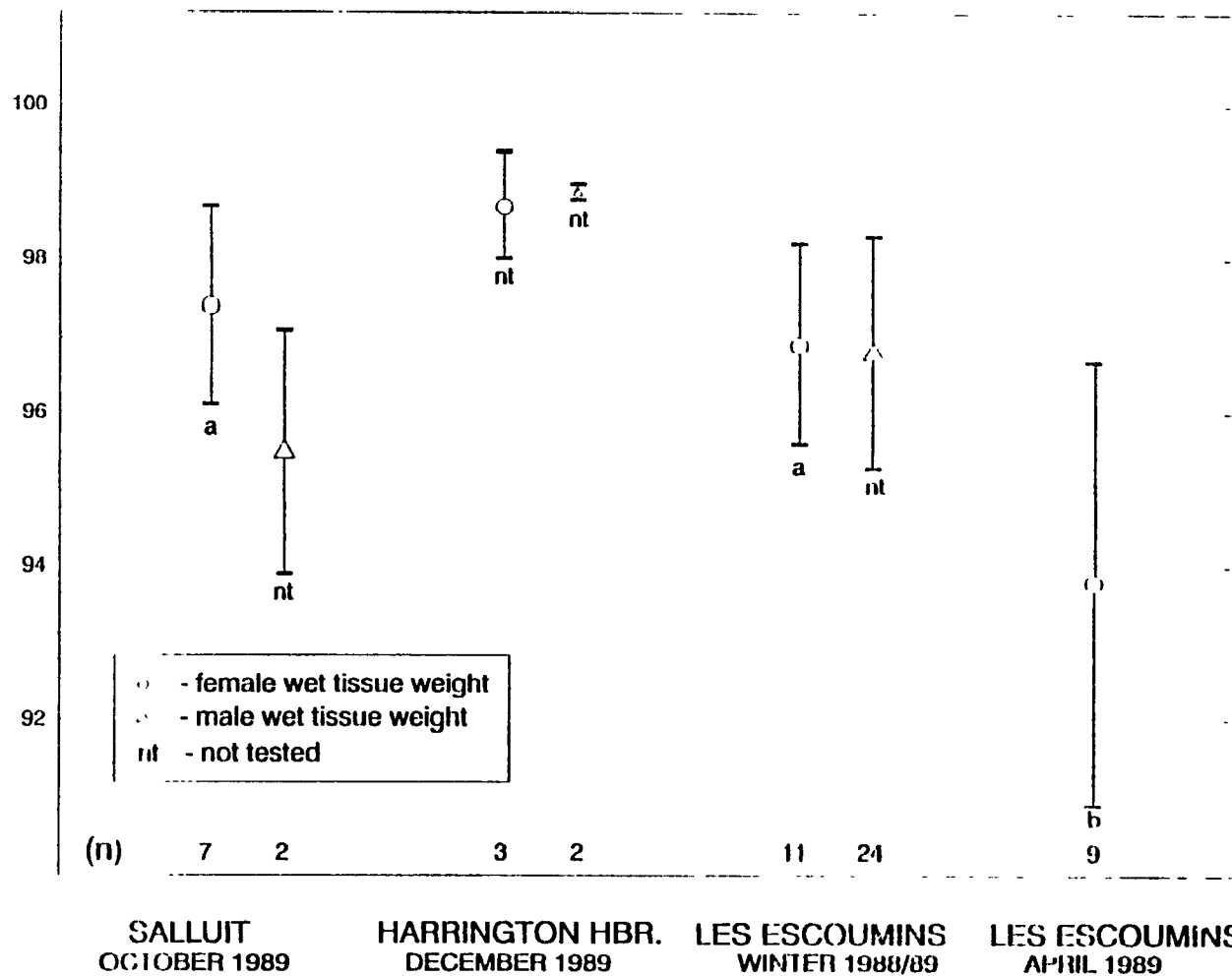


Figure 4. Seasonal and sexual variation in the lipid content of blubber tissue in harp seals. Means $\pm$ lsd, sample size (n); common subscripts represent non-significant differences in means ($\alpha=0.05$).

PERCENT LIPID IN BLUBBER TISSUE



LOCATION AND SEASON

Figure 5. Seasonal variation of core, sculp and total body mass
in female harp seals. Means $\pm$ 1 sd and sample size (n).

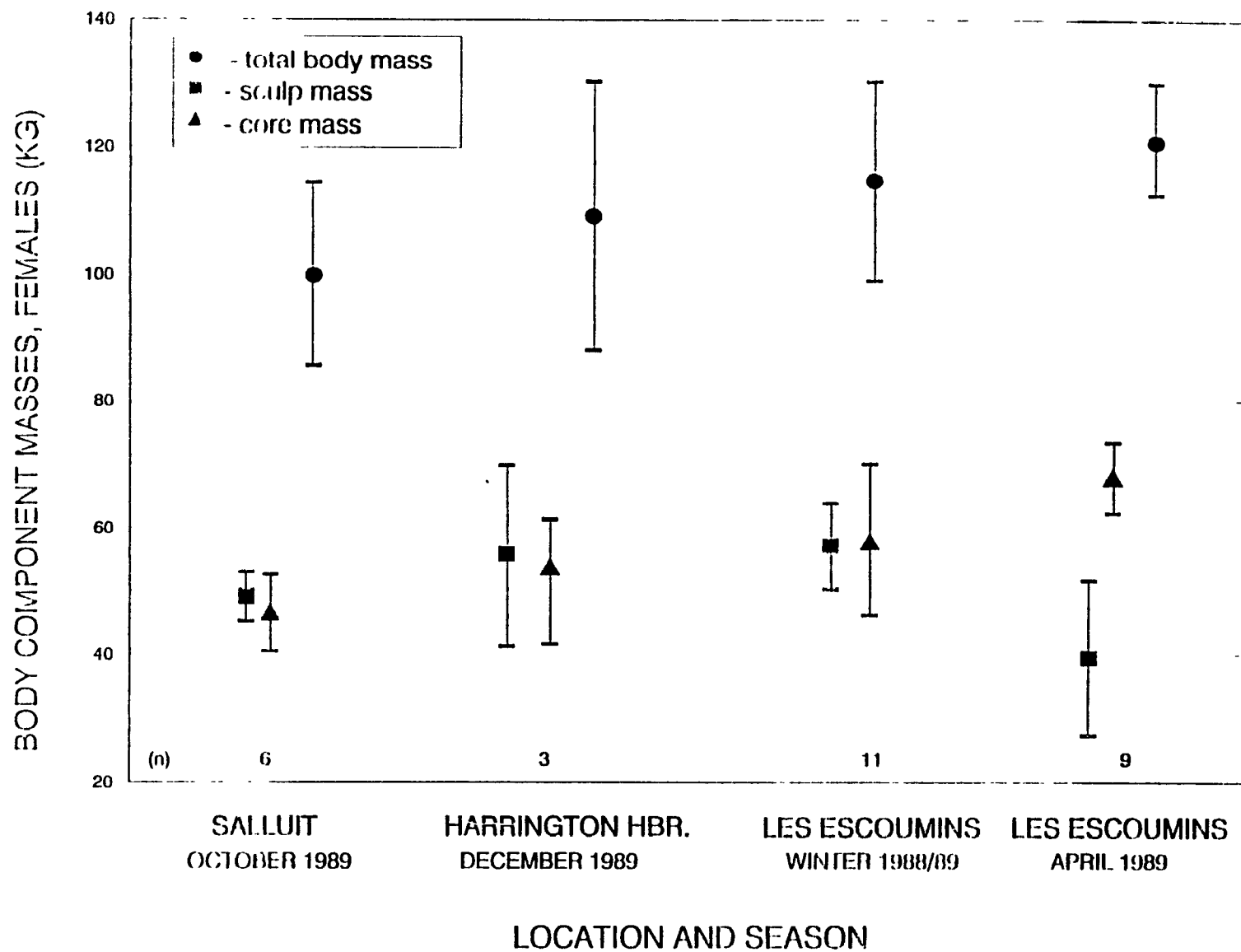


Figure 6. Seasonal variation of core, sculp and total body mass
in male harp seals. Means $\pm$ 1 sd and sample size (n).

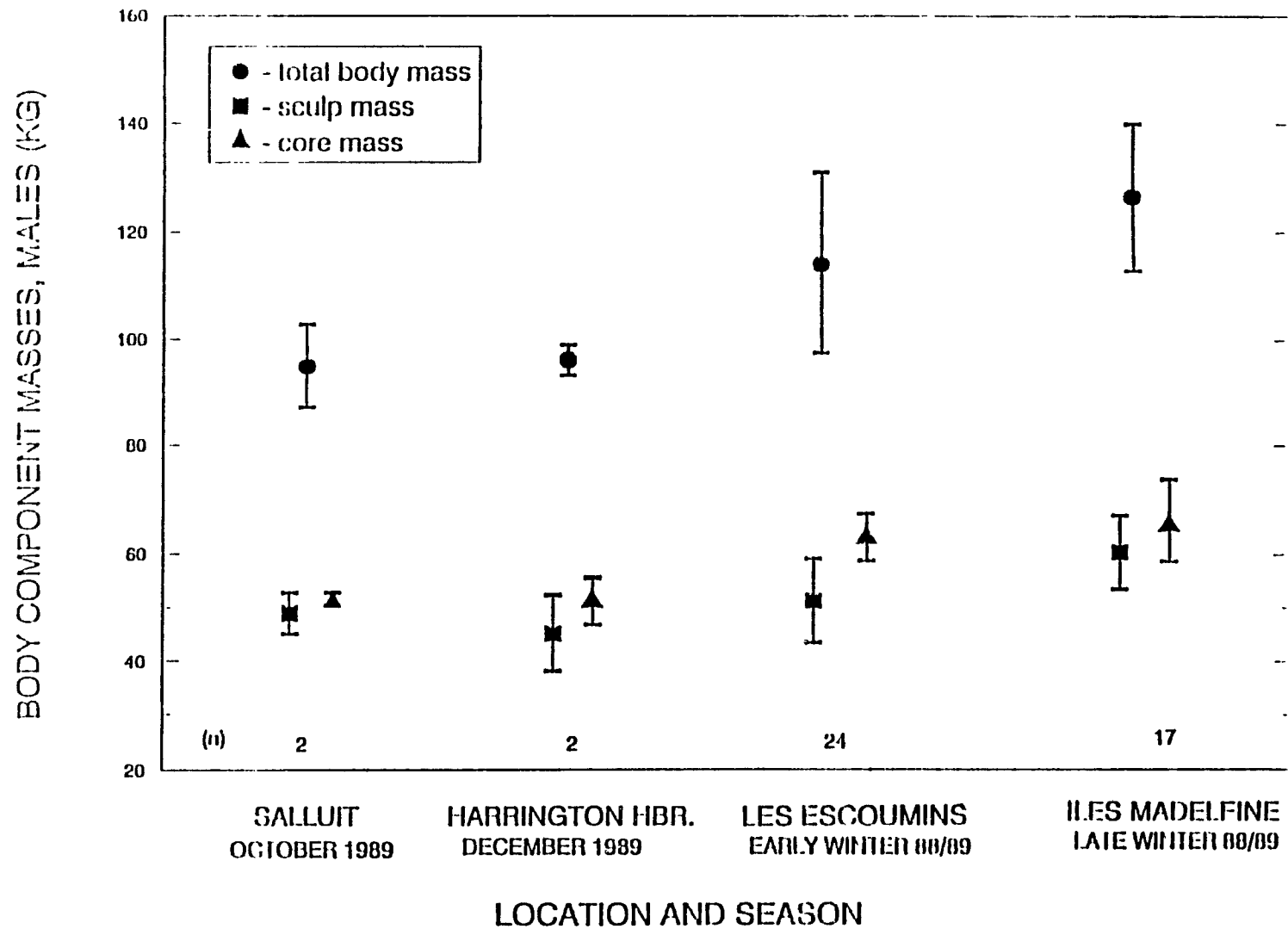
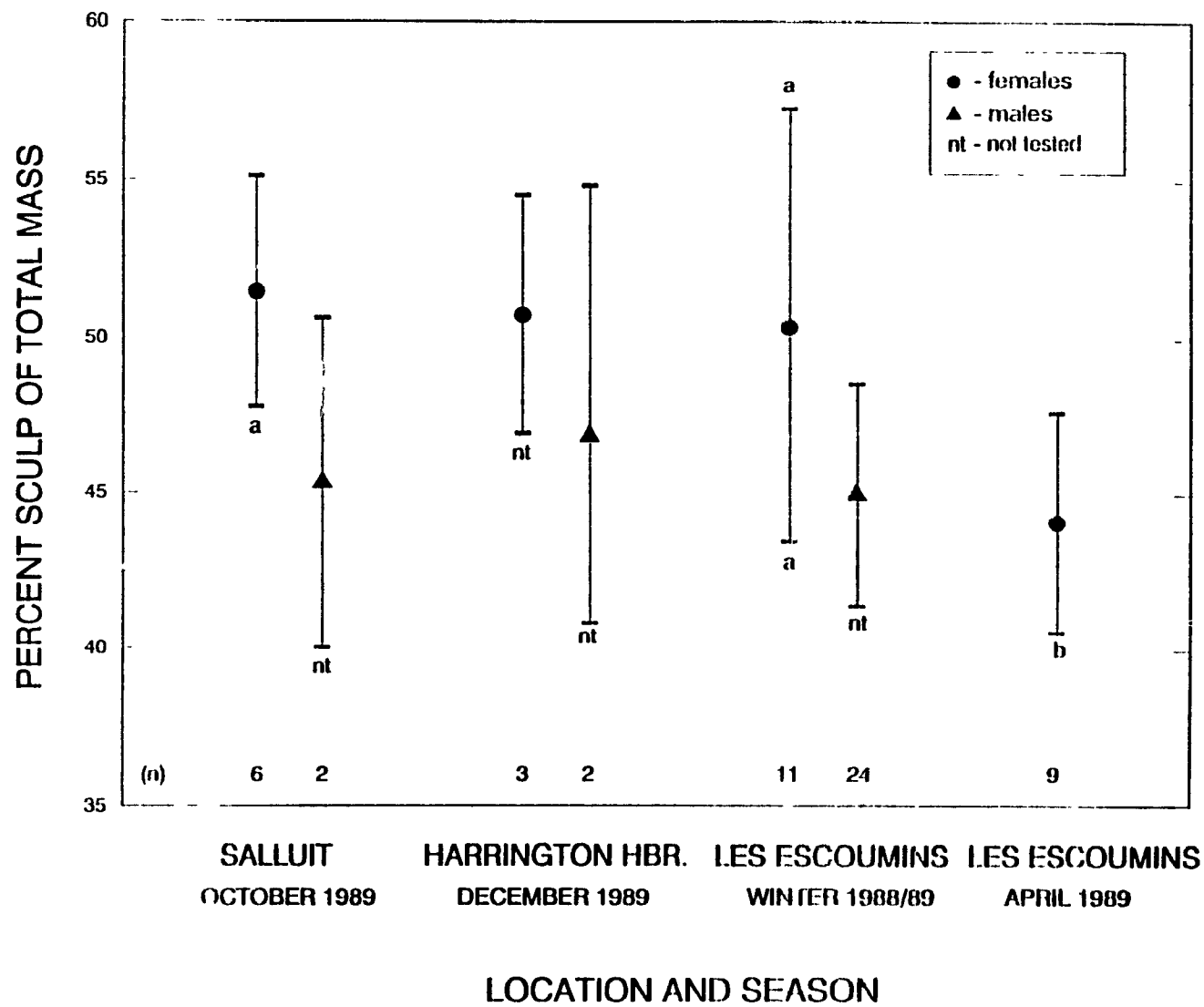


Figure 7. Seasonal and sexual variation in percent sculp of total body mass in harp seals. Means $\pm$ 1sd, sample size (n); common subscripts represent non-significant differences in means ($\alpha=0.05$).



CHAPTER IV

GENERAL CONCLUSION

GENERAL CONCLUSION

My study combines the analysis of carcass lipids with body measurements in a comprehensive evaluation of nutritional condition in the harp seal. The traditional indices of sternal blubber thickness and axillary girth/length show general trends in seasonal fatness, but are not always sensitive enough to identify significant differences in condition. Dorsal blubber thickness and girth are greatest at 50% of length and show a much stronger correlation to body fats. The direct measurement of sculp and total body mass are more labour intensive, but allow a much more detailed evaluation of condition.

The blubber serves many functions, and indices of nutritional condition reflect both stored energy and thermal insulation. Blubber mass/body mass (percent blubber content) indicates the state of thermal balance, but seasonal variation in the mass of both core and blubber limit its usefulness as an index of energy stores. The greatest store of lipids in harp seals is in the blubber (90% in winter animals), so sculp or blubber mass adjusted for length cubed provides a good indication of energy reserves. Under some field conditions, it may not be possible to measure total body mass, but sculp mass may be obtained more easily even if it must first be cut into smaller pieces.

Light feeding during the spring moult, the northward migration and, for females, the cost of lactation lead to a significant decrease in body condition. Even by mid-autumn, muscle lipid content and the mass of the core and blubber are low, but increase through the winter. Among females, those one month post-partum showed the highest lipid content in liver and muscle, reflecting very intensive feeding. This same group had significantly lower lipid in the blubber and slightly lower sculp mass. I suspect that the difference in blubber mass and lipid content is even greater immediately following lactation. When evaluating energy reserves, the seasonal variation in lipid content of blubber and other tissues should be considered.

The preference of harp seals for capelin may be related to its high caloric density relative to other fish and plankton and to its pelagic, schooling nature. The seasonal variation in feeding intensity may be related at least in part to variations in the lipid content of the prey. In both Hudson Strait and the St. Lawrence River estuary, harp seals fed primarily on capelin. The intensive feeding observed in one month post-partum females may be associated with both the reduced lipid content of capelin in spring and the need to replenish body fats lost during lactation. While harp seals in southern and arctic waters appear to specialize on particular prey types, those migrating feed on a wider variety of prey, reflecting opportunistic feeding habits.

The harp seal has been studied intensively on the breeding grounds in the Gulf of St. Lawrence, but comparatively little research has been conducted in the arctic. The low blubber and core mass in October indicate that the annual process of replenishing body mass is slow. The stored energy used during the spring migration to the arctic and the seasonally reduced fat content of capelin make summer a stressful period for the harp seal. Energy stored during winter and early spring may be essential for survival through this season.