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Estimating consumption of prey by Harp Seals (*Pagophilus groenlandicus*) in NAFO Divisions 2J3KL

Estimation de la consommation de proies par les phoques du Groenland, (*Pagophilus groenlandicus*) dans la division 2J3KL de l'OPANO

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ABSTRACT

Consumption of Atlantic Cod (*Gadus morhua*) by Harp Seals (*Pagophilus groenlandicus*) off the east coast of Newfoundland in NAFO Divisions (Div.) 2J3KL was estimated by integrating information on the numbers at age, age-specific energy requirements, seasonal distribution, and diet of Harp Seals in the Newfoundland and Labrador area. Abundance was estimated using a population model integrating pup production between the late 1970s and 2004, annual estimates of reproductive rates from 1954 to 1998, and data on age-specific removals from 1952 to 2008. Energy requirements of the population were estimated using a simple allometric model based on body mass obtained from monthly sex-specific growth curves. The proportion of energy obtained in Div. 2J3KL was estimated using data obtained from satellite telemetry and traditional tagging studies. The diet of Harp Seals in nearshore and offshore waters during winter (October – March) and spring (April – September) was determined by reconstructing the wet weight and energy content of prey in stomachs collected in 1982 and 1986 to 2007. The impact of different diet determination methods was explored by estimating consumption using a multinomial regression approach and fatty acid signatures from Harp Seal samples. Uncertainty in the consumption estimates was approximated by incorporating the uncertainty in the numbers at ages, diets, energy requirements, and seasonal distribution. Total prey consumption by Harp Seals in Div. 2J3KL during 2008 was estimated to be approximately 4.2 million metric tons. However, this estimate was imprecise with a 95% confidence interval (C.I.) being 3.2 million – 5.4 million tons. Consumption of individual prey species varied greatly depending upon the assumed diet.

RÉSUMÉ

On a estimé la consommation de morue franche (*Gadus morhua*) par les phoques du Groenland (*Pagophilus groenlandicus*) au large de la côte est de Terre-Neuve dans la division (Div.) 2J3KL de l'OPANO en intégrant les données sur les populations de phoques du Groenland selon l'âge, leurs besoins énergétiques en fonction de l'âge, leur répartition saisonnière et leur régime alimentaire dans la région de Terre-Neuve-et-Labrador. L'abondance a été estimée à l'aide d'un modèle de population qui intègre la production des blanchons entre la fin des années 1970 et 2004, les estimations annuelles des taux de reproduction de 1954 à 1998 et les données sur les prélèvements par âge de 1952 à 2008. Les besoins énergétiques de la population ont été estimés à l'aide d'un modèle allométrique simple fondé sur la masse corporelle obtenue à partir des courbes de croissance mensuelles propres à chaque sexe. La proportion de l'énergie obtenue dans la division 2J3KL a été estimée à l'aide des données tirées des télémesures satellitaires et des études de marquage traditionnelles. On a déterminé le régime du phoque du Groenland dans les eaux littorales et les eaux du large en hiver (entre octobre et mars) et au printemps (entre avril et septembre) en reconstruisant le poids humide et le contenu énergétique des proies dans les estomacs prélevés en 1982 et de 1986 à 2007. On a étudié l'effet des différentes méthodes de détermination du régime en estimant la consommation à l'aide d'une méthode de régression multinomiale et des signatures de l'acide gras relevées dans les échantillons de phoques du Groenland. L'incertitude dans les estimations de la consommation a été estimée en intégrant l'incertitude liée aux nombres selon l'âge, aux régimes, aux besoins énergétiques et à la répartition saisonnière. En 2008, la consommation totale de proies par les phoques du Groenland a été estimée à environ 4,2 millions de tonnes dans la Div. 2J3KL. Toutefois, cette estimation était imprécise avec un indice de confiance de 95 % se situant entre 3,2 millions et 5,4 millions de tonnes. La consommation des différentes espèces-proies variait grandement selon le régime supposé.

INTRODUCTION

Because of their large size and abundance, marine mammals are thought to have an important influence on the structure and function of marine ecosystems (Bowen 1997). In the northwest Atlantic, the abundance of a number of important commercial fish species have declined significantly over the past three decades. For example, the stock of Atlantic Cod (*Gadus morhua*) found in NAFO Divisions 2J3KL (i.e., 'Northern cod') has declined by over 99% since the peak in the late 1960s, and by over 90% compared to the 1980s, in spite of a moratorium and highly reduced catches since 1992 (DFO 2011a). Similarly, Capelin (*Mallotus villosus*) abundance in the same area has not recovered from a significant decline during the early 1990s (DFO 2010). During the same period, a number of marine mammal populations in the area have increased, leading to questions about the impact marine mammals, particularly seals, have had on these fish stocks. Although seals appear to have only a minor role in the collapse of groundfish stocks in the early 1990s (e.g., McLaren et al. 2001; Trzcinski et al. 2009), they may play a more important role in slowing the recovery of certain stocks (e.g., Bundy 2001; Trzcinski et al. 2006; Benoit et al. 2011).

In order to evaluate the impact of marine mammal predation on the recovery of fish stocks, information is needed on all major sources of predation and non-predation mortality, and the factors affecting recruitment. Unfortunately, however, we know relatively little about recruitment or non-predation sources of mortality. The main focus of our understanding of factors affecting recovery is on estimates of predation by a few major seal species. Therefore, much of the current discussion about the impact of seals is based upon estimates of consumption obtained from a bioenergetics model (e.g., Lavigne et al. 1985; Mohn and Bowen 1994; Hammill et al. 1995; Stenson et al. 1997; Nilssen et al. 1997; Hammill and Stenson 2000, 2002, 2004; Stenson and Perry 2001; Boyd 2002; Winship et al. 2002; Stenson and Hammill 2004). Developing a prey consumption model for seals requires information on population size, energetic requirements, diet composition, and distribution of feeding effort, as well as size classes and energy density of the prey (Harwood and Croxall 1988; Harwood 1992).

Harp Seals, *Pagophilus groenlandicus*, are the most abundant marine mammal in the northwest Atlantic (Hammill et al. 2011). They are also known to consume significant amounts of both Atlantic Cod and Capelin (Stenson et al 1997; Hammill and Stenson 2000; Stenson and Perry 2001). Therefore, it is important to estimate prey consumption by this seal species in order to determine their role in the decline and continued low abundance of these fish species. The objective of this study is to update estimates of consumption by Harp Seals in Div. 2J3KL, taking into account seasonal changes in feeding and variability in seal abundance, distribution, and diet composition. In addition, sources of uncertainty in the parameters are incorporated. These estimates can then be incorporated into multispecies models to determine the role of Harp Seals in the northwest Atlantic ecosystem.

MATERIALS AND METHODS

CONSUMPTION MODEL

Estimates of prey consumption were developed by modelling changes in population size, energy requirements, diet composition, and seal distribution. The amount of prey consumed by Harp Seals in Div. 2J3KL from 1965 to 2008 was estimated by:

$$C_{jt} = \sum_{s=1}^{s=S} \sum_{a=1}^{a=A} \sum_{i=1}^{i=I} N_{it} E_i D_{ias} P_{jas}$$

Where:

C_{jt} = Consumption of prey species *j* in year *t*.
N_{it} = Number of seals in age class *i* in year *t*.
E_i = Annual gross energy required by a seal aged *i*.
D_{ias} = Proportion of the total annual energy obtained by a seal aged *i* in area *a* during season *s*.
P_{jas} = Proportion of prey species *j* in the diet of seals in area *a* during season *s*.
I = Total number of age classes, currently 13 (ages 0 - 11 and 12+).
A = Total number of areas, currently two (inshore and offshore).
S = Total number of seasons, currently two (winter [October to March] and summer [April to September]).

The consumption model was developed as an EXCEL spreadsheet. To quantify uncertainty in consumption estimates, model parameters were assigned to statistical functions using an EXCEL add-in called @Risk (Palisade Inc). With @Risk, the model was run 1,000 times. During each run, the model samples from the assigned statistical distribution for each parameter and an estimate of consumption is generated. At the end of the 1,000 runs, the mean and standard deviation (SD) of consumption estimates were calculated.

Population

Harp Seal abundance is monitored using aerial surveys to estimate pup production. Assuming that the sex ratio is 1:1 and that pup mortality is three times that of adult mortality, total population size can be estimated by combining the pup production estimates with data on female reproduction rates and age-specific catches. Changes in population size over time are monitored by fitting the model to independent estimates of pup production (Healey and Stenson 2000; Hammill and Stenson 2003, 2005). Uncertainty (mean and SD in the numbers in each age group (0 through 11 and 12+ years)) for each year was estimated from the population trajectories provided by Hammill et al. (2011) (Fig. 1).

Energy requirements

Age-specific energy requirements were calculated using a simple allometric equation based on monthly body mass:

$$GEI_i = GP_i*(AF*293*BM_{it}^{0.75}) /ME$$

where:

GEI_i = Daily gross energy intake (kjoules/day) at age *i*.
GP_i = Growth premium (i.e., the additional energy required by young seals < age 6).
AF = Daily activity factor.
BM_{it} = Body mass (in kg) at age *i* in month *t.*
ME = metabolizable energy.

The increased energy required by younger animals primarily for growth (GP_i) was assumed to be 1.8, 1.6, 1.42, 1.26, 1.13, 1.05, and 1.0 for animals aged 0, 1, 2, 3, 4, 5, and ≥6 yrs, respectively, based on Olesiuk (1993) for Harbour Seals.

Based on studies of the energy requirements of captive and wild seals, estimates of the average daily energy requirements vary between 1.7 and 3 times (Worthy 1990) the basal metabolic rate ($293*BM_i^{0.75}$; Kleiber 1975). However, the majority of estimates indicate that a multiplier of approximately 2 is appropriate (Lavigne et al. 1982; Worthy 1990). Therefore the AF was assigned as a triangular function, with a low value of 1.7, a high of 3, and a most likely value of 2.

The proportion of ingested energy available to the seal (ME) will depend upon the type of prey eaten, generally being higher for fish than for invertebrates (Mårtensson et al. 1994; Lawson et al 1997). ME has been estimated to be 0.85 to 0.88 for juvenile Harp Seals fed herring (Keiver et al. 1984), 0.83 for Grey Seals (Ronald et al. 1984), 0.827 for Ringed Seals (Ryg and Øritsland 1991) and between 0.827 to 0.847 for Harp Seals (Lavigne et al. 1982). Lawson et al. (1997) estimated assimilation efficiencies (uncorrected for urinary loss) of Harp Seals fed various prey types to vary from 0.81 to 0.91. Based upon the diet of Harp Seals in Newfoundland and a weighted average of digestive efficiencies for various prey, Stenson et al. (1997) assumed a value of 0.83. In order to reflect the uncertainty associated with this estimate and changes in diet, we assumed that ME could be represented by a uniform function with a range of 0.8 to 0.86.

Body Mass

Growth in body mass at age *i* (BM_i) was modeled using a re-parameterized form of the Gompertz growth curve (Hammill et al. 1995):

$$BM_i = W_\infty \bullet \left(\frac{W_0}{W_\infty}\right)^{\exp\left[\frac{k_0 \bullet i}{W_0 \ln\left(W_0 / W_\infty\right)}\right]}$$

where body mass (BM_i), asymptotic weight W_∞, and weight at birth (W_0) are in kilograms, *i* is age (in years), and k_0 is the rate of growth at birth. Parameters of the growth curves (Table 1) were determined for age-mass data from animals collected in Newfoundland and along the Labrador coast using Proc NLIN (SAS Institute, 1987) (Chabot et al. 1996; Chabot and Stenson 2002, unpublished data). The uncertainty incorporated into the model was based upon the observed variance in the data.

Energy requirements vary throughout the year. To represent these differences in feeding and the storage of energy, monthly mass-at-age values were used (Table 1). Mass was assumed to be normally distributed, with mean and SD equal to the fitted values from the growth curve analysis. During the breeding and moulting periods, however, adults reduce their food intake, while pups derive all of their energy requirements from the female, stored reserves, or feed intermittently. Therefore, food intake was also allowed to vary. It was assumed that during March (breeding period), adult males, 60% of females (average proportion of females that give birth, Stenson and Wells 2011) and all pups did not forage. All juveniles and 40% of mature females were assumed to forage. In April, when animals one year of age and older (1+) are moulting and pups have reduced intake, only 50% of animals were assumed to forage.

Previous consumption estimates (e.g., Hammill and Stenson 2000) assumed that energy requirements were assumed to be constant throughout the year. For those model runs, an average body mass equal to that observed in April (Table 1) was assumed. This weight is close to the minimum weight observed and is similar to that observed in seals when they first arrive in southern waters during the fall.

Seasonal distribution

Harp Seals are highly migratory and our knowledge of their seasonal distribution is primarily based on historical catch data, tag returns, and anecdotal reports. Northwest Atlantic Harp Seals summer in the Canadian Arctic and/or West Greenland. During the fall and early winter, seals move southward along the Labrador coast. One component of this population remains off the east coast of Newfoundland/southern Labrador (i.e., Div. 2J3KL) while the other moves into the Gulf of St. Lawrence (Div. 4RS and Subdiv. 3Pn) in December. In the late spring, the animals return to the Arctic. Annual changes in ice conditions or food availability likely affect the seasonal movements of the population (Sergeant 1991). The proportion of energy obtained from various areas was assumed to be equal to the seasonal residency in that area. Following Hammill and Stenson (2000) and Stenson and Hammill (2004), residency in each area was estimated assuming that:

a) based upon the age structure of Harp Seals hunted in Greenland (Kapel 1982; Larson 1985; Anon. 1986), approximately 20% of all age groups were assumed to remain in the Arctic throughout the year. The portion remaining in the Arctic was represented by a uniform distribution and limits of 0.18 to 0.22.

b) using data obtained from satellite telemetry (Stenson and Sjare 1997), Harp Seals were assumed to leave 'southern' areas (i.e., south of Div. 2H, approximately 55°N) on July 6 (SD = 6.7 days) and return November 21 (SD = 8.1 days). These dates were assigned as normally distributed variables in the model, with mean and SD equal to these values.

c) some animals remain south all year round. This was described by a uniform distribution with limits set at 0.01 to 0.05.

d) the proportion of the animals that came south that entered the Gulf of St. Lawrence could be represented by a normal distribution with a mean of 0.26 (SD = 0.07) . This proportion is based upon the relative numbers of pups born in the southern Gulf during aerial surveys between 1990 and 2008 (Stenson et al. 1993, 2002, 2003, 2005, 2011).

e) based upon historical catch records, seal enter the Gulf of St. Lawrence on December 1 and remain there until May 1. It was assumed that variation in these dates could be represented by a normal distribution with a SD of 5 days. The remainder of the population is assumed to be present in the waters off Newfoundland (Div. 2J3KL).

f) based upon satellite telemetry data (Stenson and Sjare 1997; Stenson and Perry 2001; Stenson unpublished data), 13% of the seals in Div. 2J3KL are found nearshore (i.e.

<30 km of the headlands) during the winter (exponential distribution) while 9.4% are in the nearshore during the summer (Beta).

Diet

Average diet

The diet of Harp Seals was estimated using reconstructed wet weights of stomach contents from animals collected in nearshore and offshore waters of Div. 2J3KL between 1986 and 2007 (Fig. 2, Table 2) (Lawson et al. 1995; Lawson and Stenson 1997; Stenson and McKinnon unpublished data). Prey lengths and weights were estimated from hard parts using part length – total length and part length – and/or length – weight regression equations. If prey were intact, direct weights were recorded. If hard parts were too digested or eroded to accurately measure, an average value was calculated for that prey species based upon other individuals of the same species within the stomach or in samples from seals collected in the same year, season and location. Regression equations were obtained from published sources or stock-specific relationships where possible (Härkönen 1986; Benoit and Bowen 1990; Lidster et al. 1994; Lawson et al. 1995; Proust 1996).

Reconstructed wet weights were converted to energy densities using published energy values for each prey species (Tyler 1973; Griffiths 1977; Montevecchi and Piatt 1984; Steimle and Terranova 1985; Lawson et al. 1998). Samples were assigned to offshore and nearshore areas, as well as either the winter (October to March) or summer (April to September) season.

The average diet was calculated using all available samples and simulated data sets of total energy consumed were created using a bootstrapping (i.e., resampling-with-replacement) technique (Resampling Stats, Arlington VA, USA 1999). Each stomach was treated as a unit for resampling purposes. This process was repeated 1,000 times to generate estimates of total mass, and hence energy, from which proportions contributed by each prey group to the diet could be calculated (Table 3).

Multinomial Regression

Using an average predator diet masks any trends in prey selection. However, the available data are not sufficient to estimate diets in all year/area/season blocks for these Harp Seals. As an alternate method to estimate diets and fill in diet gaps, Koen-Alonso et al. (2009) estimated diets using a multinomial regression method (Fig. 3a,b). This method fills in data gaps by interpolating within the database.

Fatty Acid Signatures

An alternate estimate of harp seal diets was obtained from Tucker et al. (2009). This diet was estimated from the fatty acid signature of seal blubber and therefore integrated diets over a longer time frame than stomach contents (Table 4).

Diet parameters were incorporated into the model as a normally-distributed variable, with mean and SD estimated by resampling.

RESULTS

Total consumption

Assuming the average diet from 1986 to 2007, total Harp Seal consumption was estimated to have increased from approximately 807,000 (95% C.I. = 621,00 – 1,035,000) tonnes in 1965 to 4,203,000 (95% C.I. = 3,227,000 – 5,403,000) tonnes in 2008 (Fig. 4). This increase was due solely to the increase in population that occurred over this time period. Because estimates of total consumption depend upon the average energy content of the diet, they differed slightly when other diets were assumed. However, the differences were minor, although with greater uncertainty, with consumption in 2008 being slightly lower using the multinomial regression diet (4,141,000, 95% C.I. = 2,493,000 – 6,112,000 tonnes), and higher when using diets based on fatty acid signatures (4,673,000, 95% C.I. = 2,515,000 – 7,176,000 tonnes).

Consumption of individual prey species

Estimated consumption of individual prey species varied with the diet assumed. Generally, consumption estimates for individual species were highly uncertain due to the large error associated with the diet estimates.

Significant quantities of Capelin were consumed by Harp Seals in Div. 2J3KL. Assuming the average diet, Capelin consumption increased from 242,000 (95% C.I. = 181,000 – 317,000) tonnes in 1965 to 1.26 million (95% C.I. = 939,000 – 1,651,000) tonnes in 2008 (Fig. 5). Similar estimates were obtained using the multinomial model (Fig. 5). Assuming a diet obtained from the fatty acid signatures resulted in a much lower estimate of Capelin consumption with 376,000 (95% C.I. = 0 – 794,000) tonnes consumed in 2008.

Consumption of Arctic Cod (*Boreogadus saida*) increased as a function of seal population when the average diet was used. Approximately 46,000 (95% C.I. = 16,000 – 103,000) tonnes were estimated to have been consumed in 1965, rising to 239,000 (95% C.I. = 84,000 – 531,000) tonnes in 2008 (Fig. 6). Similar consumption estimates were obtained using the fatty acid diet. In contrast, a very different picture was seen when assuming the multinomial diet. Consumption of Arctic Cod increased from 204,000 (95% C.I. = 48,000 – 380,000) tonnes in 1965 to 432,000 (95% C.I. = 100,000 – 805,000) tonnes in 1986 and then declined to 45,000 (95% C.I. = 0 – 124,000) tonnes in 2008 (Fig. 6).

The estimates of Atlantic Cod consumption were highly dependent upon the diet assumed (Fig. 7). The estimates were also highly uncertain. Using the average diet, cod consumption increased from 26,000 (95% C.I. = 13,000 – 45,000) tonnes in 1965 to 134,500 (95% C.I. = 68,000 – 237,000) tonnes in 2008. The multinomial diet show very little cod consumed at the beginning of the time series but later assumes that a larger amount of cod was being taken in the offshore than seen in the raw data. As a result, cod consumption in 1965 was very low (7,000 tonnes, 95% C.I. = 0 – 17,000), but extremely high, and uncertain, in 2008 (565,000 tonnes, 95% C.I. = 75,000 – 1,112,000). Very little cod was present in the fatty acid signature data and as a result, consumption never exceeded 1,500 tonnes over the entire time period when Harp Seal diet was reconstructed using this approach.

DISCUSSION

Using a bioenergetics model similar to previous studies, I estimated total consumption of Northwest Atlantic (NWA) Harp Seals in Div. 2J3KL to be in the order of four million tonnes. These estimates of total consumption are much higher than previous (e.g., Hammill and Stenson 2000; Stenson and Perry 2001) due primarily to the higher population size of Harp Seals. In the previous studies, abundance of NWA Harp Seals was estimated to be approximately 5.5 million. Based upon additional pup production surveys and new data on reproductive rates, Hammill et al. (2011) estimate that the population increased to approximately 8.3 million seals (95% CI = 7,500,000 – 8,900,000) by 2008. As a result, the total amount prey consumed in Div. 2J3KL was proportionally higher.

Estimates of prey consumption are based on a considerable number of assumptions about population size, diet composition, spatial distribution, and energy consumption (e.g., Hammill and Stenson 2000; Stenson et al. 1997; Stenson and Perry 2001; Stenson and Hammill 2004). Stenson and Hammill (2004) examined the sensitivity of the model used to estimate consumption of NWA Harp Seals to uncertainty in the parameters using data from the northern Gulf of St. Lawrence. They found that although population size is an important factor, it is relatively well known and changes slowly (e.g., Hammill et al. 1995, 2011; Shelton et al. 1997). As a simple multiplier, the model is very sensitive to the assumptions underlying the activity factor. Unfortunately, there are relatively few studies that estimate the additional cost of activity (e.g., see Worthy 1990) and some authors have suggested that the cost of activity is greater than the range used (e.g., Nilssen et al 1997; Boyd 2002; Winship 2002), while others have suggested it may be less (Sparling and Fedak 2004). Some of these differences may be due to differing energy cost required to capture specific prey. As diets or prey abundance change, it is possible that the amount of energy required to capture sufficient prey to meet their energy needs may also vary. However, predicting the cost of obtaining prey, particularly in differing ecosystems, is extremely difficult (if not impossible) and so by using a range that encompasses most studies, I have attempted to account for differences within the uncertainty of these estimates.

A number of authors have attempted to estimate the amount of ingested energy that is actually available to seals (ME) for various prey species (e.g., Lavigne et al. 1982; Keiver et al. 1984; Ronald et al. 1984; Ryg and Øritsland 1991; Mårtensson et al. 1994; Lawson et al. 1997) and after accounting for urinary loss, the estimates were in the order of 0.8 to 0.85. However, there is a large variation among prey species and therefore, the relative proportion of different prey species will affect the overall metabolizable energy assumed. By applying a range of values for ME, these estimates account for a range of diets and contribute to the overall uncertainty in the estimates.

The average daily age specific energy requirements was assumed to be a function of body mass$^{0.75}$ multiplied by constants to account for energy requirements due to activity and growth. The body masses used to estimate energy needs were based on field data obtained from over 5,000 Harp Seals collected during the 1980s and 1990s (Chabot and Stenson 2002, unpublished data). There is some evidence that growth rates of Harp Seals were lower in the 1990s than in the 1980s (Chabot et al. 1996; Chabot and Stenson unpubl. data). If this has occurred, the energy requirements estimated for the earlier period may be negatively biases while the recent consumption would be positively biased. Preliminary results from a study of changes in winter condition between 1980 and 2008 suggest that Harp Seal body weights have continued to decline but vary greatly inter-annually. The model also assumes that seals obtain all of the energy required. In addition to changes in condition, NWA Harp Seals also appear to be showing other signs of density dependence such as reduced reproductive rates (Stenson and Wells 2011). The reduction in body mass may reflect the inability of Harp Seals to obtain all of the energy they require and could be incorporated into the model to adjust consumption estimates, particularly in more recent years. The impact of these changes in body mass on current consumption estimates needs to be explored.

Stenson and Hammill (2004) found that estimates of consumption were most sensitive to spatial and temporal variation in distribution and diet composition which is consistent with other studies (Mohn and Bowen 1996; Shelton et al. 1997; Stenson and Perry 2001). Consumption of species that are consistently important, such as Capelin, are more robust while consumption of species that are more variable in relative importance in the reconstructed diet (e.g., cod) are very sensitive to how the data are obtained.

The consumption estimates for individual prey were highly imprecise, and the three methods to reconstruct seal diets used in this study resulted in very different estimates of consumption of individual prey species. However, although specific diets varied with season, location, year, and method of estimation, forage fish such as Capelin, Arctic Cod, Sand Lance (*Ammodytes* sp.), and Atlantic Herring (*Clupea harengus*) represented the largest proportion of prey consumed. Along with these forage species, significant amounts of shrimp were consumed based upon the average contents of stomachs collected between 1986 and 2007.

Every method of diet estimation has a variety of potential biases (e.g., see Harvey 1989; Pierce and Boyle 1991; Gales and Cheal 1992; Tollit et al. 1997; Bowen 2000). The use of reconstructed wet weights tends to result in an overestimation of the ingested weight of some species (e.g., those with robust otoliths) and underestimation of other species due to differential digestion and retention rates, lack of identifiable remains from soft bodied prey, and incomplete consumption of prey (DFO 2011b). Also, determining the appropriate weights of invertebrates that may comprise an important component of the diet is very difficult (Hammill and Stenson 2000). A comparison of the diets of Grey Seals estimated from stomach contents and diets estimated from intestines suggested that otoliths of Atlantic Cod may be retained within the stomach and therefore over estimated, while smaller prey such as Atlantic Herring and Sand Lance pass through quickly and are under-represented (Stenson et al. unpublished data; DFO 2011b). The majority of biases would result in an overestimate of the proportion of Atlantic Cod in the diet (e.g. ‘belly biting’). One exception would be if Harp Seals do not consume the heads of large fish. This was observed among Harp Seals feeding on cod concentrated in a small cove but it is unknown if such behaviour occurs in open areas. Harp Seals have been seen eating very large cod intact in captive diet experiments, as well as in the wild (Lawson, pers. comm.). Examining the diet of Harp Seals using genetic methods, Marshal et al. (2010) did not find any evidence of cod in stomachs that did not also contain cod otoliths. This would suggest that if ‘belly biting’ does occur, it is not a common occurrence.

The majority of diet samples were obtained from the nearshore areas although satellite telemetry studies indicate that the majority of seals remain in the offshore (Stenson and Sjare 1997). Although fewer samples were available from offshore areas we were able to examine over 630 prey containing stomachs which gave a reasonable indication of preferred prey, particularly in Div. 2J3K which is the primary area used by Harp Seals. The multinomial model was used to draw upon information from adjacent areas to fill in the data gaps. This resulted in a much higher proportion of cod in the offshore diet than in the average diet and as a result, significantly higher estimates of cod consumption. Cod is found primarily in the stomachs of seals caught in nearshore areas of Div. 3L (Stenson unpubl. data) which is an area where bay stocks of cod are found. Extrapolating this diet to offshore areas where cod are much less plentiful is questionable and likely results in an overestimate of cod consumption using this method.

In contrast, estimates based on fatty acid signatures showed extremely low levels of Atlantic Cod in the diet and none in offshore diets (Tucker et al 2009). This method also resulted in relatively higher estimates of Sand Lance, Redfish (*Sebates sp.*), and amphipods, and lower estimates of Arctic Cod, Capelin and Atlantic Herring than either of the methods using the reconstructed stomach contents. The reason for the large differences found between the diets obtained from stomach contents and that obtained using fatty acid signatures is unknown. The fatty acid signatures of Grey Seals on the Scotian shelf also indicated much lower levels of Atlantic Cod in the diet than faecal samples (DFO 2011b). It is not clear if the difference is due to the longer feeding time frame represented by the blubber or is a characteristic of the method. Fatty acid signatures are a relatively new technique (e.g., Iverson et al. 1997) and the usefulness of the method to identify specific prey species has been questioned. Also, potential biases inherent in the method have not been examined in detail.

Comparing the consumption estimates from the different diet reconstruction approaches is difficult since each method represents different aspects of Harp Seal feeding. The average diet integrates the total samples collected over the study time period. Variation in the diet among years is represented by the total sample variance. As such, the diet is assumed to be relatively constant over time with no trends in prey selection and changes in consumption are due to changes in population size. However, some changes in diet did occur. For example, no Atlantic Cod were seen in the stomach samples prior to 1987 while Arctic Cod declined after the mid 1990s. In contrast, shrimp and Sand Lance appear to have increased in recent years. Using annual estimates of diet capture some of these changes, but these data are only available for nearshore areas. The multinomial regression technique uses the available data to model the proportions of different prey species in the diet as a function of year, location, season, and age. This method allows us to fill in data gaps and reflect trends in consumption. The diets obtained from the multinomial regression model appeared to be very similar to the annual reconstructed diets in areas where samples were numerous (e.g. winter Div. 2J3K). However, this approach may have difficulties accurately estimating diets in areas where sampling is infrequent, particularly if prey availability differs from areas where data are abundant. Fatty acid signatures (Iverson et al. 1997; Tucker et al. 2009) integrate diet over longer time periods and are easy to obtain from live animals. Harp Seals build up blubber reserves during the fall and winter as they migrate south from their Arctic feeding grounds. Although they do feed a little during the breeding and moulting period, they utilize the energy in the blubber until they begin to feed intensively the following spring. Prey species identified in the blubber were consumed over this entire time period which may cause a problem if it is necessary to assign a diet in a specific areas or season to determine consumption of a specific prey stock. The use of fatty acid signatures also requires an extensive prey reference library and the identification of integration correction factors in order to estimate species composition.

Although Harp Seals consume a significant amount of prey in Div. 2J3KL, they are not the only important predator in the region. Hooded Seals (*Cystophora cristata*) are the second most abundant pinniped in the northwest Atlantic. They are much less abundant than Harp Seals (~600,000, Hammill and Stenson 2006), but larger in size. Hammill and Stenson (2000) estimated that Hooded Seals consumed 362,900 tonnes of prey, primarily Greenland Halibut and Atlantic Cod, in Div. 2J3KL during 1996. Approximately 25 species of cetaceans are seasonal residents within Div. 2J3KL. Based upon a 2007 survey of cetaceans on the Canadian continental shelf south of 60°N (Lawson and Gosselin 2009), Lawson (unpubl. data) estimated that the more abundant cetacean species consume approximately 2 million tons of prey which is half of the amount estimated for Harp Seals.

Although the total amount of prey consumed by marine mammals appears to be very large, the most important predators in Div. 2J3KL are other fish. Depending upon the assumptions used, Koen-Alonso (unpubl. data) estimates that fish consume from 2.5 to 10 times as much prey as Harp Seals. Understanding the impact of all sources of predation is important if we wish to understand the northwest Atlantic ecosystem.

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Table 1. Model parameters mean (SE) for male and female growth parameters, where AS is asymptotic mass (kg), birth is mass at birth (kg), and growth rate is $kg \cdot y^{-1}$.

		Males			Females		
Month		AS	Birth	Growth Rate	AS	Birth	Growth Rate
November	Mean	117.4	32.9	10.38	120.9	26.9	11.95
	SE	3.05	1.84	0.61	2.43	2.07	0.52
December	Mean	114.7	32.5	11.48	123.7	30.4	11.61
	SE	2.66	2.3	0.69	2.79	2.3	0.67
January	Mean	143.5	43.7	10.94	133.4	40	10.98
	SE	4.49	5.34	1.21	9.01	5.03	1.75
February	Mean	145.8	31.1	11.61	133.6	21.7	12
	SE	3.06	3.88	0.67	5.05	5.81	0.98
March	Mean	131	37.8	13.38	123.5	19	15.84
	SE	2.25	6.33	1.27	1.63	6.44	1.28
April	Mean	102.6	34.2	11.27	98.6	30.8	12.3
	SE	1.04	1.28	0.45	1.26	1.21	0.49
May-June	Mean	90.2	31.1	6	98.8	27.5	6.2
	SE	3.07	1.01	0.41	3.71	1.19	0.45

Table 2. Spatial and temporal distribution of Harp Seal stomach samples from NAFO Div. 2J3KL (Fig. 2).

	Nearshore				Offshore				
	Div. 2J3K		Div. 3L		Div. 2J3KL		Div. 3L		
Year	Summer	Winter	Summer	Winter	Summer	Winter	Summer	Winter	Total
1982-89	356	1,353	12	29		13			1,763
1990-99	501	1,760	114	190	57	76	94	39	2,831
2000	37	204	6	13	9	3			272
2001	61	223	7	7	0	0			298
2002	49	126	8	9	0	14			206
2003	12	157	6	9	0	0			184
2004	26	128	3	8	97	23			285
2005	68	205	4	9	0	9			295
2006	67	111	13	4	0	48			243
2007	52	102	8	1	26	29			218
Total	1,229	4,369	181	279	189	215	94	39	6,595

Table 3. Average diet composition of Harp Seals in Div. 2J3KL based upon samples collected between 1986 and 2007. Diet is expressed as percent energy contribution. Diet samples were bootstrapped 1,000 times to determine mean and SD.

	Winter				Summer			
	Nearshore		Offshore		Nearshore		Offshore	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
American Plaice	0.15	0.06	2.18	1.49	0.93	0.33	3.38	2.40
Amphipod	0.30	0.05	1.14	0.33	0.23	0.06	0.74	0.20
Arctic Cod	43.15	1.51	0.78	0.17	16.01	1.67	0.52	0.15
Atlantic Cod	12.87	1.33	0.67	0.32	8.17	1.33	1.75	0.94
Atlantic Herring	12.99	0.88	0.10	0.10	21.46	1.86		
Bird	0.08	0.04			<0.01	<0.01		
Capelin	12.64	0.64	46.81	4.85	33.84	2.02	44.46	5.20
Euphausiid	0.44	0.05			2.56	0.27	<0.01	<0.01
Gadoid sp.	0.05	0.01	<0.01	<0.01	0.02	0.01	0.16	0.16
Gadus sp.	1.17	0.22			0.90	0.31	0.32	0.33
Greenland Halibut	0.52	0.12	2.40	0.97	0.65	0.23	1.05	0.47
Lumpfish		0.00						
Mysid	0.19	0.08	<0.01	<0.01	0.26	0.06		
Other Fish	4.47	0.40	4.01	1.96	6.60	2.00	2.57	1.48
Other Invert	0.02	0.01	<0.01	<0.01	0.12	0.11	0.02	0.01
Pleuronectidae	0.36	0.10	1.28	0.77	1.77	0.38	7.38	3.64
Redfish sp.	0.02	0.02	0.47	0.32	0.47	0.29	0.04	0.03
Rock Cod	2.50	0.29			1.40	0.35		
Salmon					0.09	0.09		
Sand Lance	1.40	0.19	0.03	0.03	0.66	0.21	19.18	3.13
Sculpin	2.49	0.40	0.66	0.25	0.62	0.20	0.45	0.14
Shrimp	3.59	1.57	38.81	4.89	2.04	0.25	17.70	2.98
Smelt	0.16	0.07			0.13	0.12		
Squid	0.39	0.06	0.67	0.19	1.05	0.21	0.25	0.10
White Hake	0.02	<0.01			0.05	0.05		

Table 4. Diet composition of Harp Seals in Div. 2J3KL based upon fatty acid signatures (from Tucker et al. 2009).

	Winter				Summer			
	Nearshore		Offshore		Nearshore		Offshore	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
American Plaice	0.10	0.47	0.27	1.54	0.90	2.27	0.52	1.74
Amphipoda	25.65	22.71	40.00	33.11	23.12	14.16	22.41	17.57
Arctic Cod	10.29	17.58	5.99	11.07	8.74	8.34	3.88	8.42
Atlantic Cod	0.10	0.57	<0.01	0.03	0.48	1.28		
Capelin	17.89	18.32	10.92	13.34	10.41	6.76	14.60	16.22
Gadidae	1.01	4.19	1.58	4.34	1.49	2.21	6.17	9.41
Greenland Halibut	0.17	1.09	0.07	0.28	0.33	0.90	0.52	1.73
Herring	8.73	16.27	6.55	14.01	9.03	9.86	9.73	15.38
Lumpfish	0.10	0.67	0.15	0.80	0.43	1.23	0.05	0.24
Redfish	7.32	11.19	9.38	16.64	15.91	13.98	23.09	22.51
Salmon	0.12	0.49	0.42	1.06	0.45	0.79	0.72	1.28
Sand Lance	25.09	20.02	21.12	20.55	24.03	14.28	16.16	17.39
Squid	0.06	0.52	0.20	0.82	0.10	0.26	0.25	1.12
Winter Flounder	0.58	1.92	0.53	1.87	1.07	1.58	0.67	2.13
Other fish	2.55	7.14	2.94	6.67	3.70	4.51	1.26	2.23

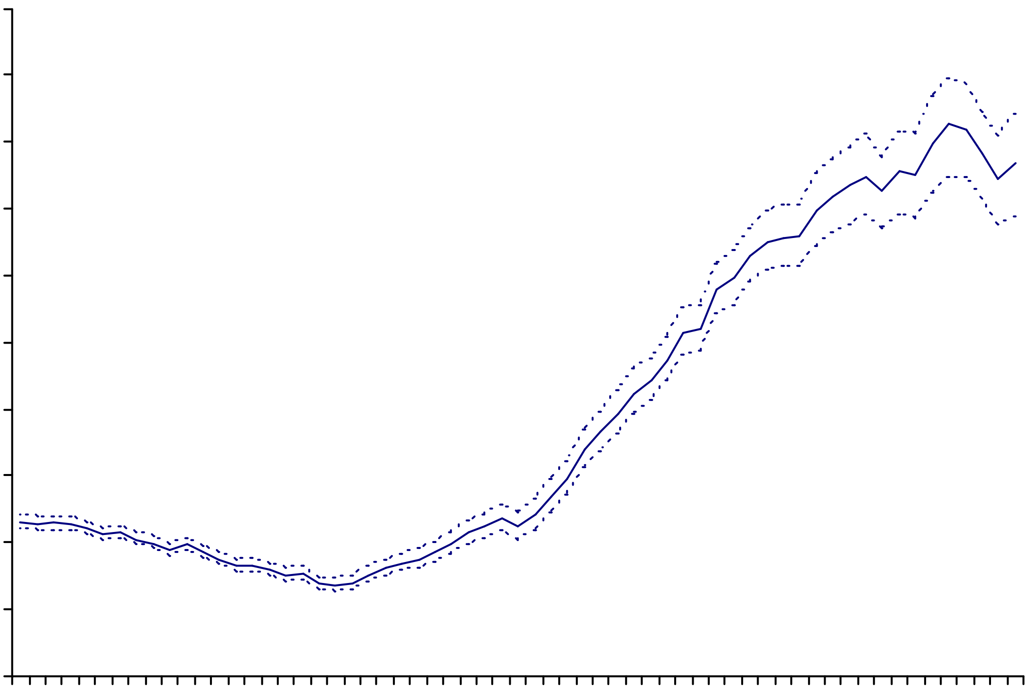

Figure 1. Harp Seal (± 95% C.I.) abundance in the Northwest Atlantic (from Hammill et al. 2011).

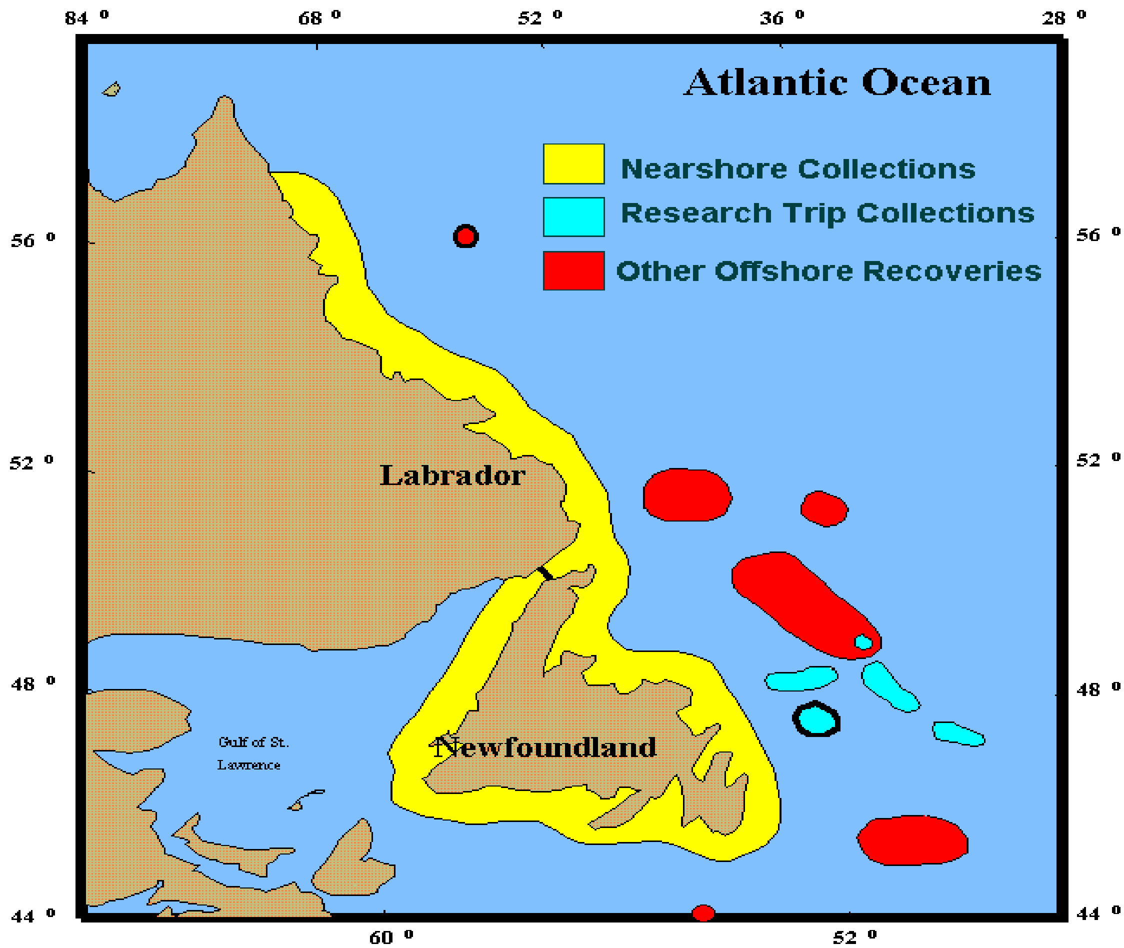

Figure 2. Location of main sampling locations to determine diets of northwest Atlantic Harp Seals.

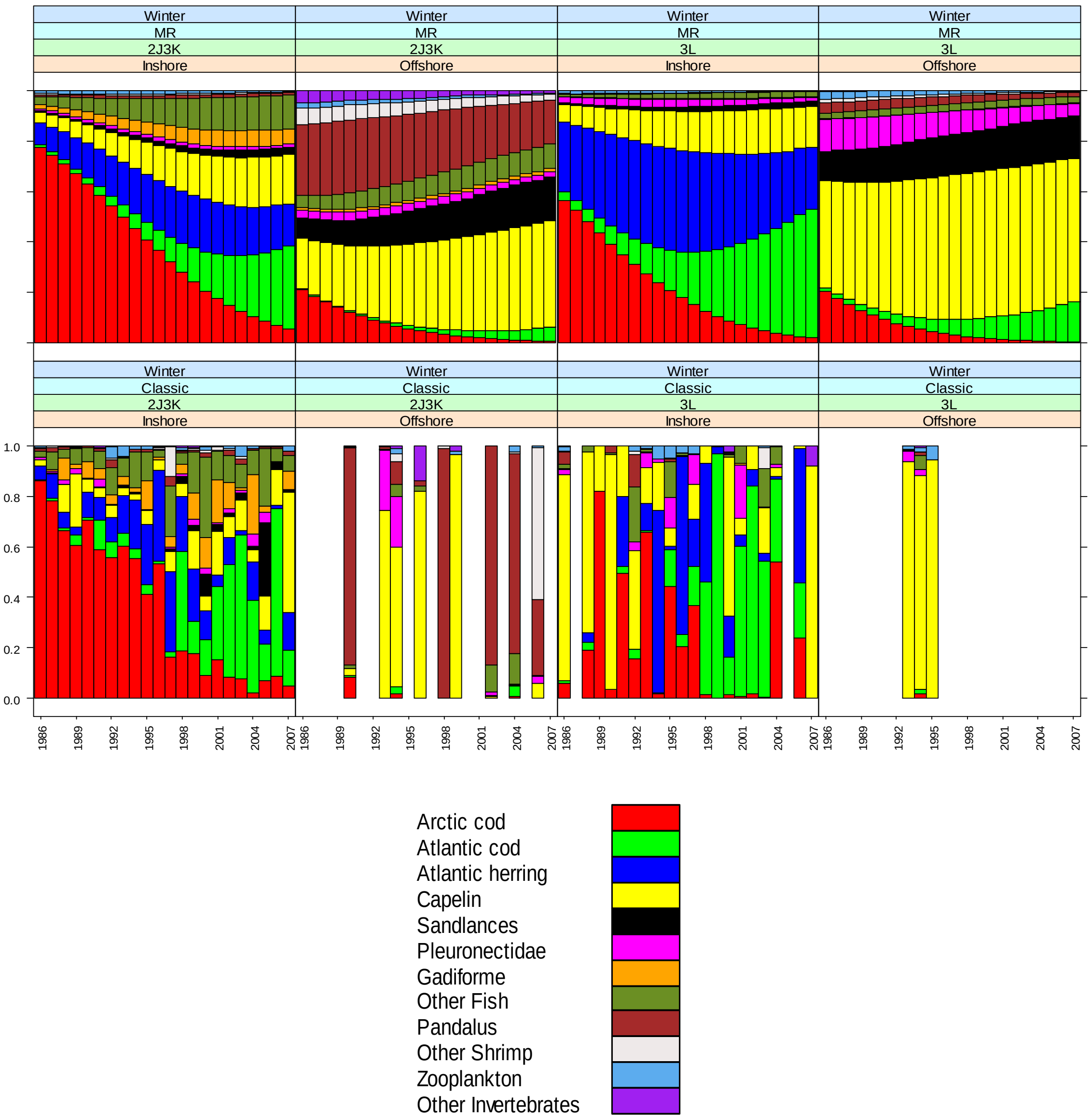

Figure 3a. Estimated winter diets of Harp Seals in Div. 2J3KL determine using a multinomial regression method (from DFO 2009).

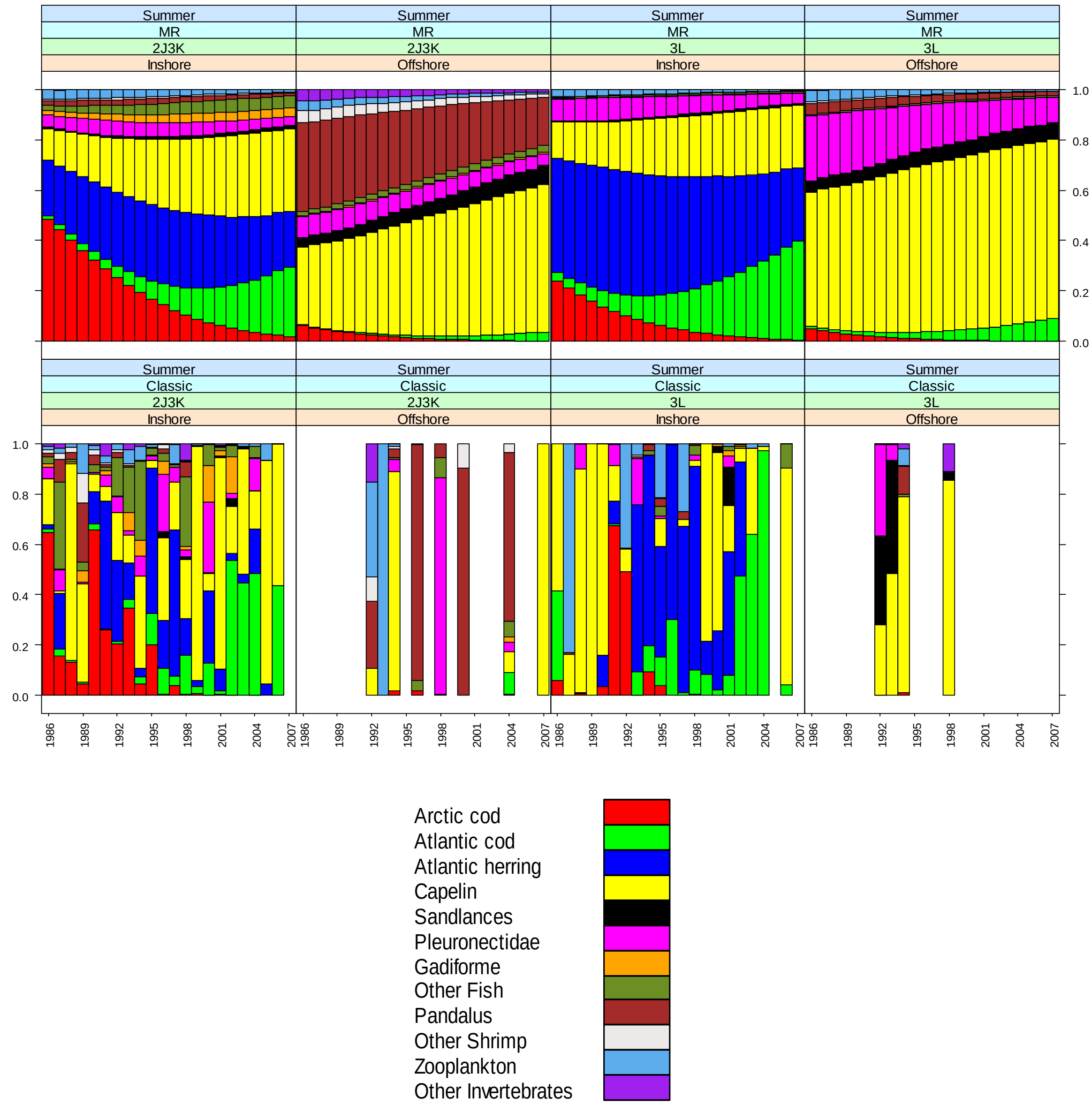

Figure 3b. Estimated summer diets of Harp Seals in Div. 2J3KL determine using a multinomial regression method (from DFO 2009).

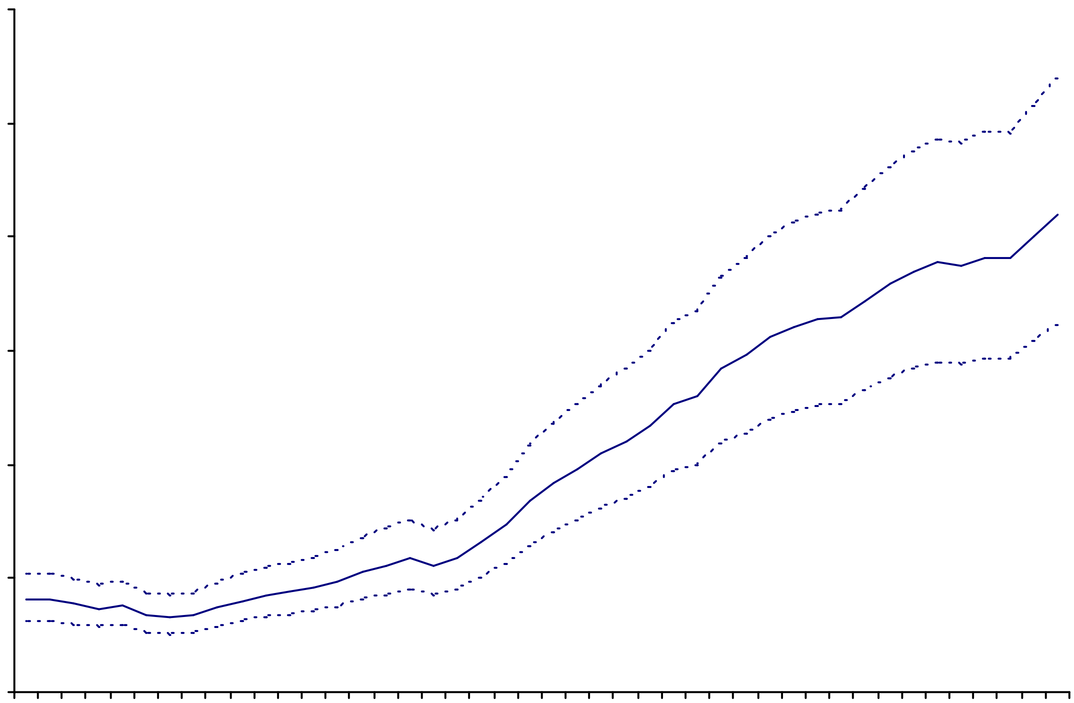

Figure 4. Total consumption (mean + SD) of prey by Harp Seals in Div. 2J3KL, 1965 to 2008, estimated assuming an average diet from 1986 to 2007.

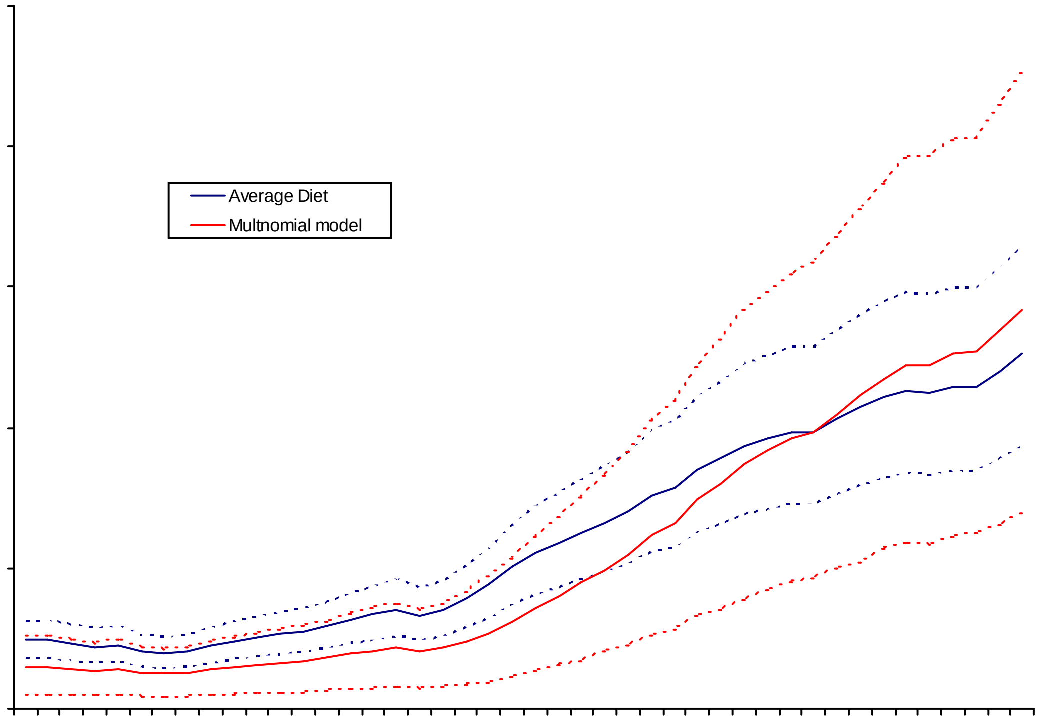

Figure 5. Estimated (mean, 95% C.I.) Capelin consumption by Harp Seals in Div. 2J3KL, 1965 to 2008, assuming an average diet from 1986 to 2007 and a diet obtained from a multinomial model.

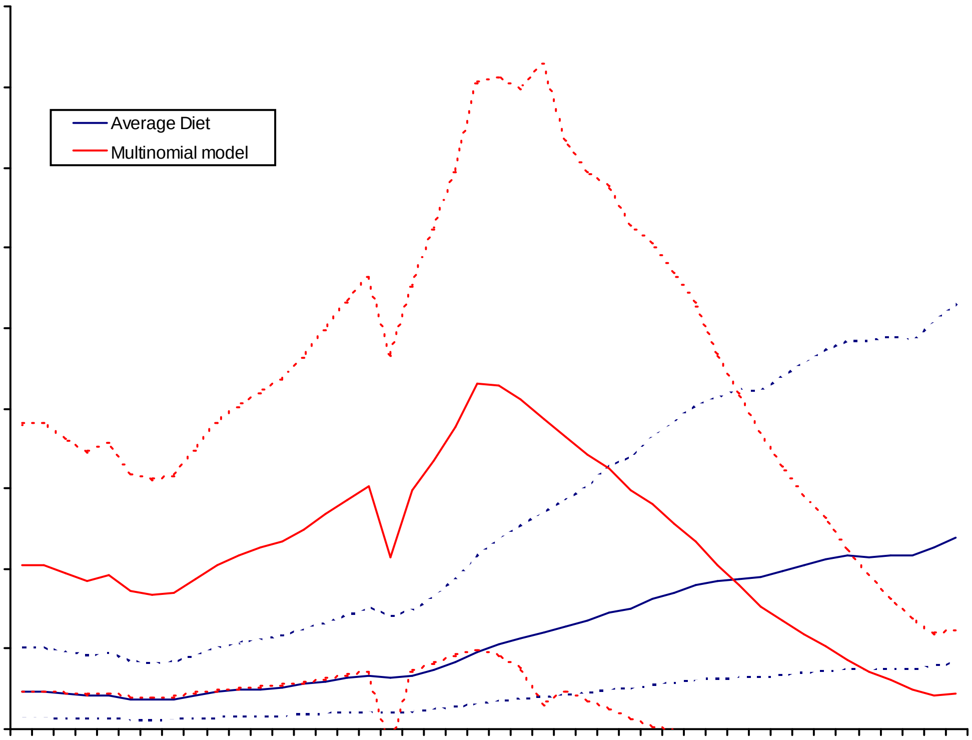

Figure 6. Estimated (mean, 95% C.I.) Arctic Cod consumption by Harp Seals in Div. 2J3KL, 1965 to 2008, assuming an average diet from 1986 to 2007 and a diet obtained from a multinomial model.

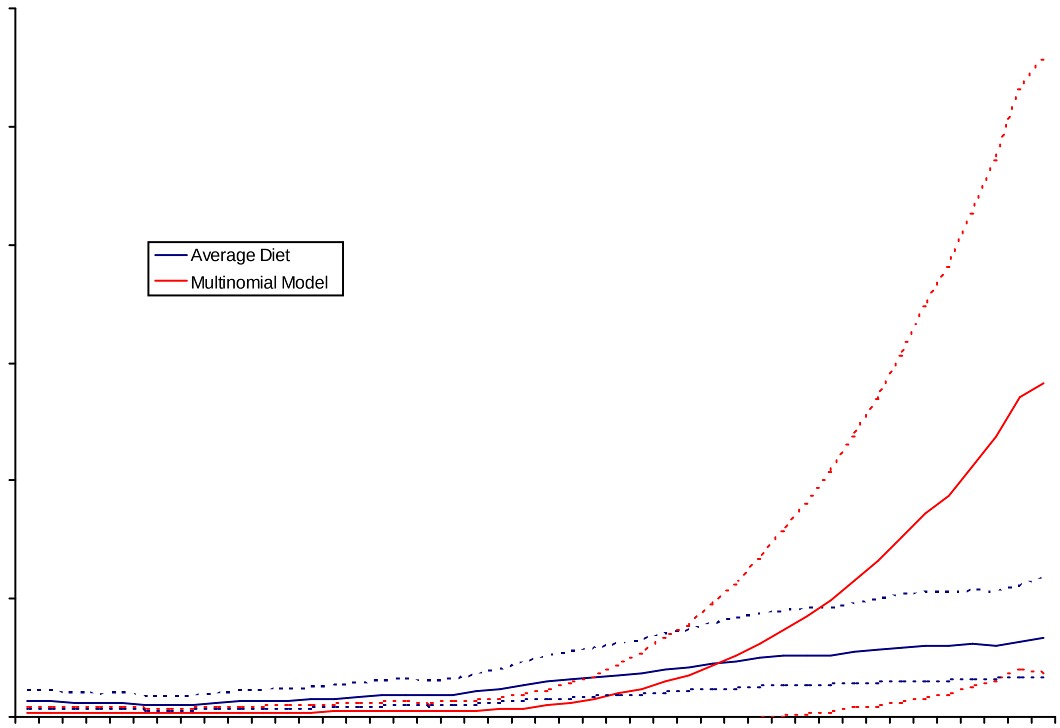

Figure 7. Estimated (mean, 95% C.I.) Atlantic Cod consumption by Harp Seals in Div.2J3KL, 1965 to 2008, assuming an average diet from 1986 to 2007 and a diet obtained from a multinomial model.