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Research Document 2004/089

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Document de recherche 2004/089

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Quantifying uncertainty in estimates of Atlantic cod (*Gadus morhua*) consumption by harp seals (*Phoca groenlandica*)

Quantification de l'incertitude dans les estimations de la quantité de morues (*Gadus morhua*) consommées par les phoques du Groënland (*Phoca groenlandica*)

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ISSN 1499-3848 (Printed / Imprimé)

Canada

Abstract

The decline in many groundfish stocks in Atlantic Canada has raised concerns about the role of seals in the Northwest Atlantic ecosystem. Estimates of consumption by predators are one piece of information that is required in order to determine the impact predators are having on the recovery of cod stocks. The objective of this paper is to describe the model used to estimate prey consumption by harp seals and to assess the sensitivity of estimate to model parameters. Consumption of Atlantic cod by harp seals in the northern Gulf of St Lawrence (NAFO zone 4RS3Pn) was estimated for the period 1985-2003. Estimates were obtained by combining information on harp seal abundance, energy requirements, diet composition and the distribution of animals. Consumption of Atlantic cod in 2003 was estimated to be in the order of 27,000 (SD = 6,800) tonnes. Current estimates differ from earlier studies by attempting to incorporate variability in population estimates, energy requirements, seal distribution, and diet composition. Sensitivity analysis indicated that the model was most sensitive to changes in population size, the parameters required to estimate energy requirements (ME, AF, body mass), the proportion of seals that enter the Gulf and the length of winter residency. Assumptions about the proportion of animals that remain throughout the year in the Arctic or southern waters had little impact on the estimates of cod consumption.

Résumé

La baisse de l’effectif de nombreux stocks de poissons de fond au Canada atlantique a soulevé des préoccupations quant au rôle des phoques au sein de l’écosystème de l’Atlantique Nord-Ouest. Les estimations de la quantité de morues consommées par des prédateurs représentent une partie de l’information nécessaire pour déterminer l’incidence de ceux-ci sur le rétablissement des stocks de morue. L’objectif du présent rapport est de décrire le modèle utilisé pour estimer la quantité de morues consommées par les phoques du Groënland et d’évaluer la sensibilité des estimations aux paramètres du modèle. La quantité de morues consommées par les phoques du Groënland dans le nord du golfe du Saint-Laurent (zones de l’OPANO 4RS3Pn) a été estimée pour la période de 1985 à 2003. Les estimations ont été obtenues en combinant les données sur l’abondance, les besoins en énergie, la composition du régime alimentaire et la répartition des phoques du Groënland. La quantité de morues consommées en 2003 a été estimée à environ 27 000 tonnes (écart-type = 6 800). Les estimations actuelles diffèrent de celles effectuées lors d’études antérieures parce qu’elles tentent d’incorporer la variabilité des données sur l’abondance, les besoins en énergie, la répartition et la composition du régime alimentaire des phoques. Une analyse de sensibilité a révélé que le modèle est plus sensible aux variations de la taille de la population, aux paramètres nécessaires pour estimer les besoins en énergie (énergie métabolisable, facteur d’activité et masse corporelle), à la proportion de phoques qui entrent dans le golfe du Saint-Laurent et à la durée de leur séjour en hiver. Les hypothèses sur la proportion de phoques qui passent l’année dans l’océan Arctique ou dans les eaux du sud ont eu peu d’incidence sur les estimations de la quantité de morues consommées.

Introduction

Because of their large size and abundance marine mammals are thought to have an important influence on the structure and function of some marine ecosystems (Bowen 1997). This has lead to the view that seals can have a negative impact on commercial fisheries. Over the last decade several Atlantic groundfish stocks have collapsed. Within the northern Gulf of St Lawrence (NAFO zone 4RS), estimated biomass of 3+ cod declined from over 600,000 t in the mid-1980's to around 25,000 t in the early 1990's while the biomass of Northern Cod in the waters off eastern Newfoundland (NAFO zones 2J3KL) are estimated to be 1% or less of the average biomass during the 1980s (DFO 2004a, b). This decline coincided with marked increases in seal populations throughout the region, leading to suggestions that seals were involved in failure of the fishery.

It is now considered that seals played only a very minor role in the collapse of groundfish stocks in the early 1990's (McLaren et al. 2001), but may play a more important role in slowing the recovery of certain Atlantic cod stocks (Bundy 2001). In a recent review of seal management, McLaren et al. (2001) concluded that cod consumption by seals in NAFO zone 4RS3Pn and 2J3KL was large compared to biomass estimates suggesting that seal predation was a substantial component of the high mortality experienced by these stocks. Owing to the large amount of uncertainty involved in the estimates they were reluctant to go further in evaluating impact.

In order to evaluate the impact of seal 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, we know very little about recruitment or the levels of predation by all but a few 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 1996 Hammill et al. 1995; Stenson et al. 1997; Nilssen et al. 1997; Hammill and Stenson 2000; Stenson and Perry 2001; Boyd 2002; Winship et al. 2002). 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). Although data exist to quantify some of these parameters, many are poorly understood or based on limited data. As a result, consumption models usually require a large number of assumptions of unknown quality which can change as new data become available. Although there are a few exceptions (e.g. Boyd 2002; Winship et al. 2002), the large degree of uncertainty associated with the assumptions and parameters used to generate the consumption estimates has rarely been considered (Stenson and Perry 2001). Stenson and Perry (2001) and Hammill (2000) incorporated some uncertainty into estimates of prey consumption by harp seals off Newfoundland and in the northern Gulf, but efforts to date have been limited.

Here, we model fish consumption by harp seals, taking into account seasonal changes in feeding and variability in seal abundance, distribution, and diet composition. In addition, we incorporate all possible sources of uncertainty in these estimates and examine the impact of these assumptions on our estimates of total consumption. The model is developed using harp seals in the Gulf of St. Lawrence. Our overall objective is to examine the general approach to estimating consumption and how uncertainty might be incorporated into the model.

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 NAFO Divisions 3Pn and 4RS from 1985 - 2000 were 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} = No. of seals in age class i in year t.
E_{i} = Annual gross energy required by a seal aged i.
D_{ias} = Prop.of the total annual energy obtained by a seal aged i in area a during season s.
P_{jas} = Prop. of prey species j in the diet of seals in area a during season s.
I = Total no. of age classes, currently 13 (ages 0 - 11 and 12+).
A = Total no. of areas.
S = Total no. of seasons, currently 2 (Winter and Summer)

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 500 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 500 runs, the mean and 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 3 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). Uncertainty (mean and standard deviation in the numbers in each age group (0 through 11 and12+) for each year was estimated from the population trajectories provided by Healey and Stenson (2000)(Fig. 1).

Energy requirements

Energy requirements were assumed to be constant throughout the year as in earlier presentations (Hammill and Stenson 2000) and to also vary by month.

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

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

where:

GEI_i = Daily gross energy intake (kjoules/day) at age i,
GP, = Growth premium (i.e. the additional energy required by young seals < age 6).
AF = Daily activity factor
BM_i = Body mass (in kg) at age i
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 - 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 – 0.847 for harp seals (Lavigne et al. 1982). Lawson et al. (1997) estimated assimilation efficiencies (uncorrected for urinary loss) of harp seal fed various prey types to vary from 0.81 – 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 associate 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 kg, 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. In previous runs of the model, energy requirements were assumed to be constant throughout the year. For these 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.

Model simulations were also carried out assuming energy requirements vary throughout the year. To represent differences in feeding and the storage of energy, monthly mass at age values were used in the energy requirement equation (Table 1). They were assigned as normally distributed variables in the model, with mean and SD equal to the fitted values from the growth curve analysis. However, during the breeding and moulting periods adults reduce their food intake, while pups derive all of their energy requirements from the female, stored reserves or feed intermittently. In the constant energy model, no changes in consumption were incorporated into the model, as these were accounted for by the average weights used. In the variable energy model that incorporated monthly changes in body mass, food intake was also allowed to vary. It was assumed that during March (breeding period), adult males, 60 % of females 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.

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. 2J3KL) while the other moves into the Gulf of St. Lawrence 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), residency in each area was estimated assuming that:

a) based upon the age structure of harp seals hunted in Greenland (Anon. 1986, Kapel 1982, Larsen 1985), 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 0.18-0.22.

b) using data obtained from satellite telemetry (Stenson and Sjare 1997), harp seals were assumed to enter 'southern' (i.e. south of NAFO division 2H, approximately 55^0 N) on July 6 (SD=6.7 days) and leave November 21 (SD=8.1 days). They 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 also described by a uniform distribution with limits set at 0.01-0.05.

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=.07) . This proportion is based upon the relative numbers of pups born in the southern Gulf during aerial surveys in 1990, 1994 and 1999 (Stenson et al. 1993, 2002, 2003).

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.

f) The distribution of animals within the Gulf was assumed to vary by month (Table 2).

Diet

The diet of harp seals was estimated using reconstructed wet weights of stomach contents from animals collected along the Lower North Shore from Harrington Harbour (Dec-Feb: N=24 in 1999, N=9 in 2000) and from Godbout (N=20 in 2000; N=18 in 1996) and along the west coast of Newfoundland and the lower North Shore (N=782 between 1986 and 2002) (Table 3) (Lawson *et al*. 1995; Hammill unpublished data; Stenson 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) when available. For 4R cod the otolith (OL)– Fork length (FL) regression used was:

$$FL_{cm} = 6.1520 + 0.7341\,(OL_{mm}) + 0.1323\,(OL^{2}_{mm})$$

The cod length-weight regression equation:

$$FM = 10^{(-5.2106 + 3.0879 * LOG_{10}(FL))} * 1000$$

where FM is fish mass (in gm) and FL is fork length (in cm).

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 either a winter (October – March) or Summer (April – September) season.

Diet samples were grouped according to location (4S, 4Rd or 4Rabc/3Pn) (Fig. 2) and season of collection. An 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 (Effron 1979). Each stomach was treated as a unit for resampling purposes. This process was repeated 1000 times to generate estimates of total mass and hence energy, from which proportions contributed by each prey group to the diet could be calculated. Annual diets were also determined if a sample contained a minimum of four stomachs for NAFO zones 4R. In both cases diet parameters were incorporated into the model as a normally distributed variable, with mean and SD estimated from the bootstrapped means in the case of the average diet or from the sample means in the case of the annual diets.

Sensitivity analysis

To determine the sensitivity of the model estimates to parameter assumptions, the model output was compared to the base run after altering model parameters by 20%.

Results

In NAFO zone 4S, diet samples were obtained from December to February in 1996, 1999 and 2000. The pooled, bootstrapped diet was dominated by capelin, sand lance and euphausiids, which accounted for a total of 82 % of diet intake in terms of energy. Atlantic cod accounted for only 2% of the total diet (Table 4).

In NAFO zones 4R/3Pn there was sufficient information to divide the samples into two zones, 4Rabc and 4Rd/3Pn, and two seasons October-March and April-September. In the bootstrapped diet, Atlantic herring and capelin were the two most important prey species in 4Rabc accounting for ≥ 66% of the diet by energy, while cod accounted for ≤ 8% of the diet (Table 4). In NAFO zone 4Rd/3Pn, Atlantic cod dominated the diet, accounting for an average of 21% of the diet during April-September and 42% of the diet during October-March. Herring and capelin were also important prey species, particularly during April-September (Table 4). In the current analyses, the proportion of cod was lower in most regions or periods of the year compared to the 2001 assessment due in part to larger sample sizes. In 4S, the proportion of cod was much lower due to the inclusion of samples from Godbout, which is as at the eastern extremity of the St. Lawrence estuary in NAFO zone 4S (Table 4).

Annual changes in diet composition show considerable inter-annual variability in the contribution of cod and herring to the overall diet in both zones 4Rd/3Pn and 4Rabc (Table 5). Insufficient data were available for 4S to consider annual changes in diet.

Consumption of cod using the 2004 diet composition and distribution of animals was about 20% lower than estimates presented in 2001. The estimates were also more precise than in previous runs of the model. Cod consumption using the 2004 model increased from about 17,043 tonnes (SD=4,357) in 1985 to 27,666 tonnes (SD=7,139) in 2003. Using the 2001 model, cod consumption increased from 21,108 tonnes (SD=14,971) in 1985 to 34,223 tonnes (SD=24,331) in 2003 (Table 6; Fig. 3). Estimates of cod consumption by harp seals obtained using the constant energy budget model were essentially the same ($\text{Mean}_{2004\ \text{constant}}$=27,666 t, SD=7,139 vs $\text{Mean}_{2004\ \text{variable}}$=27,044 t, SD=6,784) as estimates obtained from the model that incorporated seasonal changes in body mass and food intake (Table 6; Fig. 3).

Consumption using these average diets was compared to consumption estimates using annual diets; seasons were treated separately, because of differences in sample sizes (Tables 7,8; Figs. 4,5). Unfortunately, suitable numbers of diet samples (n>3) are not available for all years. The proportion of cod in the diet varied considerably between years in NAFO zones 4Rabc and 4Rd/3Pn (Table 5). Throughout the time series, annual estimates of cod consumption showed considerable inter-annual variability and very high variance. The standard deviations of the estimates from the annual diets were quite large owing to the small sample sizes. However, consumption estimates obtained using the average diets lay within 1 SD of the annual estimates. Estimated total consumption in NAFO zone 4R obtained from annual diets alone was 12, 620 tonnes (SD=11,483), in 1996, 10,865 tonnes (SD=11,515) in 1997, 37,554 tonnes (SD=28,896) in 1999 and 12095 tonnes (SD=16,663) in 2001.

The sensitivity of the model was examined by comparing model output, after altering model parameters by 20%, with output from the basic runs. Model output was most sensitive to changes in population size, the parameters required to estimate energy requirements (ME, AF, body mass), the proportion of seals that enter the Gulf and the length of winter residency (Table 9). The proportion of animals in NAFO zone 4Rd/3Pn and the proportion of cod in their diet were also important. Assumptions about the proportion of animals that remain throughout the year in the Arctic or southern waters had little impact on the estimates of cod consumption. Assumptions about the residency of seals and their diet in 4S and 4Rabc also had only a minor impact on the estimates.

Discussion

These estimates of cod consumption by harp seals are based on a considerable number of assumptions about population size, diet composition, spatial distribution, and energy consumption (Hammill and Stenson 2000, Stenson et al 1997, Stenson and Perry 2001). Previous work has indicated that pinniped population size was the most important factor affecting fish consumption estimates (Hammill et al. 1995; Shelton et al. 1997; Stenson *et al*., 1997). However, population size is relatively well known and changes occur relatively slowly from year to year

The model is also sensitive to changes in the estimated energy requirements. We assumed that average daily age specific energy requirements of seals were a function of body mass$^{0.75}$ multiplied by constants to account for energy requirements due to activity and growth. Variability in the age-mass relationships was incorporated into the analyses, as well as seasonal changes in energy requirements. The body masses used to estimate energy needs were based on field data obtained from over 5,000 harp seals (Chabot and Stenson 2002, unpublished data). There is some evidence that growth rates of harp seals may have declined in recent years (Chabot et al 1996, Chabot and Stenson unpublished data). If this has occurred, the energy requirements estimated by our model may be overestimated.

Accounting for monthly changes in energy requirements had little impact on the overall consumption. Specific costs associated with reproduction, were not included, but these add only about 5% to the total energy requirements of the population (Olesiuk 1993; Hammill et al. 1999). Furthermore, some of these costs would have been accounted for by the monthly changes in body mass. At the same time, harp seals feed very little during the breeding season and during the moult and independent foraging by pups is limited during the first 4-8 weeks of their lives. Incorporating these changes, the overall energy required during the winter period increased, while that needed during the spring was reduced. However, due to differences in the residency patterns and diet in these two seasons, total consumption remained essentially the same.

Energy requirements are also affected by the constants applied to the energy intake model. We assigned a triangular function to the Activity Factor, with a maximum value of 3, and a most likely value of 2. As a simple multiplier, the model is very sensitive to this assumption. There are only a 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 (e.g. Nilssen et al 1997, Boyd 2002, Winship et al. 2002) while others have suggested it may be less (Sparling and Fedak 2004). However, we have remained with a value of 2, because there is no evidence that harp seals have higher annual energy requirements than other similar sized mammals (Lavigne et al. 1986; Innes et al. 1987). At the same time, we did not include any factor for metabolic depression, which acts to reduce energy requirements during periods of fasting (Øritsland and Markussen 1990).

The amount of ingested energy that is actually available to the animal (ME) assumed in the model has a significant impact on the consumption estimates. A number of authors have attempted to estimated this value 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 – 0.85. However, there is a large variation among prey species and therefore, the relatively proportion of different prey species will affect the overall metabolizable energy assumed. We apply a range of values for ME but do not adjust this for different diets. The impact of modifying this to reflect variation in the diets is unknown.

Two variables which show the greatest variability, temporal/spatial changes in distribution and temporal/spatial changes in diet composition, are the two variables for which we have the least information. Large changes in diet composition can occur across years, seasons and geographical areas as shown by our limited diet data. This is consistent with other studies (Mohn and Bowen, 1996; Shelton *et al*., 1997; Stenson sand Perry 2001). Using annual diet estimates result in highly variable estimates of yearly consumption. However, these estimates usually fell within the range of consumptions obtained using an average diet, particularly in 4R/3Pn. Because of the high variance, none of the annual consumption estimates were significantly different than the estimates derived using the average diet. This variance was due to the highly imprecise estimates of cod in the diet. Although many of these diet estimates were based upon small sample sizes, sample size alone could not account for the high variance as even samples with >30 stomachs were associated with high standard deviations. It will be difficult to estimate consumption of cod (which make of a small proportion of the diet) precisely because the occurrence of cod in the diet appears to be highly variable regardless of sample size.

We have attempted to account for the uncertainty in the diet samples, but have not addressed potential bias. The vast majority of samples were colleted in nearshore areas and we have applied them to the entire area under consideration. Harp seals collected in nearshore and offshore areas along the east coast of Newfoundland (NAFO area 2J3KL) have very different diets (Lawson et al. 1995, 1998; Lawson and Stenson 1997; Stenson and Perry 2001). If a similar situation occurs in the northern Gulf of St. Lawrence, the diets used may be inappropriate.

During December to June there are approximately 1,000,000 harp seals in the Gulf of St Lawrence. Given the large number of animals, the model is sensitive to the general distribution between the NAFO zones. Harp seals appear to enter the Gulf primarily via the Strait of Belle Isle (Sergeant 1991) and move along the north shore dispersing towards the Magdalen Islands, the Estuary and the west coast of Newfoundland. Although McLaren et al (2001) felt that diet sampling was biased towards a few communities, these communities tend to develop seal hunting traditions because seals are abundant. Strong hunting traditions of harp seals, particularly along the Quebec Lower north shore, indicate that seals are abundant in these nearshore areas, while the absence of autumn commercial sealing along the Newfoundland west coast or a seal hunting tradition along the Newfoundland south coast indicates a lower abundance or absence of animals in these areas.

Within the Gulf, consumption estimates are particularly sensitive to the proportion of animals distributed between the northern (4Rabc) and southern (4Rd/3Pn) areas of 4R owing to the marked differences in the composition of the harp seal winter diet in these areas. This zone is not considered an important overwintering area for harp seals. The limited satellite telemetry and aerial survey data indicates that harp seals remain in 4T after whelping, move into the St Lawrence estuary or occupy northeastern 4S/4Ra (Hammill and Stenson unpublished data; J.-F. Gosselin Pers. Comm.). An absence of large numbers of seals taken traditionally in this area during the early winter months also indicates that seals may not concentrate in this area.

The proportion of harp seals that remain in the Arctic during the winter or remain in southern waters during the summer is unknown. Therefore, we have had to make reasonable assumptions as to the extent. Fortunately, estimates of consumption in the Gulf of St. Lawrence are relatively insensitive to these assumptions.

The current estimate of cod consumption in NAFO zone 4Rs3Pn is approximately 27,000 (SD = 6,800). This is lower, and more precise, than previous estimates (Hammill 2000). The primary reason for this change appears to be the inclusion of improved diet data and slight changes in residency. As more information is obtained it is expected that changes will continue to occur in these estimates.

Estimates of fish consumption by seals in Atlantic Canada have been available since the 1980’s (Lavigne et al. 1985; see Hammill and Stenson 2000 and Stenson and Perry 2001 for additional references). Over time, estimates have been refined as information on population size, energy requirements and diet composition has improved. However, there remains a considerable amount of uncertainty associated with these estimates. Incorporating variability into the model as a statistical function represents one approach to taking into account this uncertainty. As more information is obtained, these functions can be modified with relative ease. Understanding the magnitude of the bias associated with current estimates of consumption remains a significant challenge. The lack of good information on the spatio-temporal distribution of animals has an important impact on local abundance, and the appropriate diet that must be applied to estimate consumption. Without this information it is not possible to determine in what direction our estimates may be biased.

Estimating consumption of fish by seals is only one component in the complex question of evaluating the impact of pinnipeds on commercial fisheries. Other information needed to understand impact include quantifying the contribution of seal consumption to total natural mortality, understanding how mortality would vary with changes in abundance of the seal and the prey populations (i.e. the functional form of the predator-prey relationship) and a need to understand whether the removal of the pinniped predator would result in a direct benefit to the prey population or whether an alternative predator or source of mortality might assume a greater role . Also, it is important to determine how mortality relates to factors limiting recruitment in prey populations. Until we understand these, the role seal predation has on the recovery of cod cannot be determined.

Acknowledgements

We thank Dave McKinnon (Nfld) and Pierre Carter (Qc) who completed much of the diet reconstructions.

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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·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. Monthly distribution of harp seals in the northern Gulf of St Lawrence assumed by Hammill and Stenson (2002) and in the present study.

Area	Jan	Feb	March	April	May	June	July	Aug	Sept	Oct	Nov	Dec
2001												
4Rabc	0.12	0.096	0	0.01	0.05	0.02	0.02	0.02	0.02	0.02	0.02	0.12
4Rd/3Pn	0.03	0.024	0	0.04	0.20	0.08	0.08	0.08	0.08	0.08	0.08	0.03
4S	0.20	0.15	0.20	0.20	0.25	0.45	0.45	0.45	0.45	0.45	0.45	0.20
4T	0.50	0.58	0.70	0.65	0.35	0.40	0.40	0.40	0.40	0.40	0.40	0.50
4Vn	0.05	0.05	0.05	0.05	0.05	0	0	0	0	0	0	0.05
3Ps	0.10	0.10	0.05	0.05	0.1	0.05	0.05	0.05	0.05	0.05	0.05	0.10
Present												
4Rabc	0.12	0.10	0.02	0.10	0.20	0.10	0.10	0.05	0.05	0.05	0.05	0.12
4Rd/3Pn	0.04	0.03	0.01	0.01	0.06	0.01	0	0	0	0	0	0.04
4S	0.45	0.35	0.25	0.40	0.45	0.68	0.85	0.95	0.95	0.95	0.95	0.45
4T Estuary	0.25	0.20	0.15	0.20	0.10	0.10	0.05	0	0	0	0	0.25
4T South	0.10	0.29	0.55	0.25	0.15	0.10	0	0	0	0	0	0.10
4Vn	0.01	0.01	0.01	0.01	0.01	0	0	0	0	0	0	0.01
3Ps	0.03	0.02	0.01	0.03	0.03	0.01	0	0	0	0	0	0.03

Table 3. Monthly and Annual distribution of harp seal stomach samples from NAFO zones 4R and 3Pn (Fig 2).

Year	Jan	Feb	Mar	Apr	May	June	July	Aug	Nov	Dec	Grand Total
4Rabc											
1986					5						5
1989					3						3
1990				3							3
1991						5					5
1992				1	14		3				18
1993					23	17	1				41
1994				3	15						18
1995				1	3	10					14
1996		7	18			5	1			14	45
1997	8				5	5				20	38
1998	3				7		7			24	41
1999			3		3	3			2	23	34
2000					10				7	18	35
2001					1	11	1			30	43
2002					2	10	1				13
Total	11	7	21	8	91	66	14		9	129	356
4Rd/3Pn											
1989			2	2							4
1990		2	8	1	4						15
1991				17	3						20
1992	1	6	7	5	14	3		1	1		38
1993		4	5	29	11	1					50
1994	6		1	30	18	2					57
1995	1			1	14	2			1	1	20
1996		7	16	3	20	4				13	63
1997	14		1	5	17	9				2	48
1998	13	1								8	22
1999	9		2		4					11	26
2000	12	2		1		1				25	41
2001	3		3		4					10	20
2002	1	1									2
Total	60	23	45	94	109	22		1	2	70	426

Table 4. Average diet composition of harp seals in NAFO zones 4S, 4Rabc and 4Rd/3Pn by season used in the 2001 cod stock assessment and the current study. Energy contribution to the diet is expressed as a proportion. Diet samples were bootstrapped 1000 times to determine mean and SD.

	4Rabc				4Rd/3Pn				4S	
	Apr – Sept		Oct - Mar		Apr - Sept		Oct - Mar		Jan - Dec	
	Av	SD	Av	SD	Av	SD	Av	SD	Av	SD
2001										
Atlantic Cod	0.109	0.025	0.035	0.013	0.203	0.043	0.372	0.083	0.060	0.135
Atlantic Herring	0.175	0.031	0.257	0.038	0.114	0.039	0.208	0.106	0.016	0.040
Capelin	0.319	0.045	0.500	0.040	0.227	0.053	0.023	0.013	0.272	0.369
Euphausiid	0.003	0.001	0	0	0	0	0.002	0.002	0.080	0.027
Gadoid sp.	0	0	0	0	0	0	0.012	0.007	0.006	0.002
Gadus sp.	0.002	0.001	0.005	0.002	0.001	0.001	0.023	0.009	0.040	0.013
Redfish sp.	0	0	0	0	0.083	0.044	0.203	0.042	0	0
Rock Cod	0.010	0.003	0	0	0	0	0.003	0.002	0	0
Salmon	0.005	0.004	0	0	0	0	0	0	0	0
Sand Lance	0.043	0.012	0.027	0.006	0.270	0.061	0.019	0.013	0.258	0.052
Other prey	0.333		0.177		0.102		0.136		0.267	
2004										
Atlantic Cod	0.08	0.01	0.03	0.01	0.21	0.05	0.42	0.07	0.02	0.01
Atlantic Herring	0.29	0.04	0.57	0.10	0.12	0.04	0.18	0.08	0	0
Capelin	0.37	0.04	0.12	0.03	0.22	0.06	0.02	0.01	0.48	0.06
Euphausiid	0	0	0	0	0	0	0	0	0.08	0.03
Gadoid sp.	0	0	0	0	0	0	0.01	0.01	0.01	0.00
Gadus sp.	0	0	0	0	0	0	0.02	0.01	0.04	0.01
Redfish sp.	0	0	0	0	0.08	0.04	0.20	0.04	0	0
Rock Cod	0.01		0	0	0	0	0	0	0	0
Salmon	0.01		0	0	0	0	0	0	0	0
Sand Lance	0.04		0.03	0.01	0.27	0.06	0.02	0.01	0.26	0.05
Other prey	0.19		0.25		0.09		0.12		0.11	

Table 5. Average proportion (and SD) of cod in annual diet samples (n) of harp seals in NAFO zones 4R and 3Pn

Year	4Rd / 3Pn						4Rabc					
	April - September			October - March			April - September			October - March		
	n	Av	SD	n	Av	SD	n	Av	SD	N	Av	SD
1986							5	0.007	0.015			
1990	4	0.788	0.319	10	0.278	0.449						
1991	21	0.136	0.306				5	0	0			
1992	23	0.137	0.308	15	0.112	0.223	18	0.054	0.231			
1993	40	0.075	0.221	9	0.236	0.373	41	0.043	0.149			
1994	50	0.110	0.270	7	0.020	0.052	18	0.093	0.251			
1995	17	0.052	0.216				14	0.115	0.273			
1996	27	0.066	0.182	35	0.462	0.417	5	0	0	39	0.002	0.010
1997	31	0.060	0.209	17	0.174	0.267	10	0.106	0.190	27	0.014	0.029
1998				21	0.437	0.442	14	0.049	0.126	27	0.099	0.231
1999	4	0.372	0.527	22	0.452	0.407	6	0.298	0.394	28	0.117	0.237
2000				39	0.282	0.338	9	0.059	0.176	25	0.063	0.158
2001	4	0.052	0.104	16	0.248	0.375	13	0.003	0.012	30	0.070	0.167
2002							13	0.274	0.381			
Average	209	0.210	0.045	191	0.417	0.065		0.085	0.098		0.061	0.046

Table 6. Cod consumption (tonnes) using diet and distributions from 2001 assessment, revised diet and distribution for 2004 assessment and revised 2004 diet and distribution data and using a variable energy intake model.

	2001 model, constant energy intake		2004 model constant energy intake		2004 model, variable energy intake	
	Ave	SD	Ave	SD	Ave	SD
1985	21,108	14,971	17,043	4,357	16,742	4,251
1986	22,682	16,075	18,249	4,703	17,962	4,608
1987	24,002	16,986	19,291	4,990	19,017	4,900
1988	24,942	17,706	20,025	5,171	19,724	5,070
1989	25,614	18,185	20,546	5,299	20,220	5,194
1990	26,599	18,854	21,363	5,490	21,003	5,398
1991	27,791	19,714	22,310	5,698	21,924	5,592
1992	29,101	20,655	23,388	6,016	22,979	5,840
1993	30,358	21,538	24,389	6,244	23,993	6,165
1994	31,847	22,568	25,580	6,574	25,165	6,506
1995	33,093	23,558	26,537	6,828	26,118	6,738
1996	34,292	24,429	27,522	7,092	27,082	6,966
1997	34,241	24,322	27,522	7,109	27,048	6,888
1998	34,245	24,277	27,552	7,076	27,072	7,011
1999	34,150	24,300	27,530	7,080	26,988	6,870
2000	34,218	24,239	27,674	7,176	27,072	6,895
2001	34,249	24,367	27,687	7,244	27,039	6,857
2002	34,311	24,451	27,649	7,120	27,049	6,868
2003	34,223	24,331	27,666	7,139	27,044	6,784

Table 7. Atlantic cod consumption (tonnes) by harp seals in NAFO zone 4Rabc estimated using bootstrapped diet based on all years combined for each season (October-March or Apr-September) and annual diets.

Year	October - March				April – September			
	Average cod diet		Annual diet		Average cod diet		Annual diet	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
1985	1,304	445			2,183	604		
1986	1,400	479			2,332	647	201	449
1987	1,483	509			2,462	683		
1988	1,539	528			2,554	711		
1989	1,579	541			2,622	731		
1990	1,638	558			2,727	758		
1991	1,711	585			2,852	799	0	0
1992	1,793	611			2,991	836	2,010	9,066
1993	1,871	641			3,118	864	1,587	5,730
1994	1,963	673			3,271	914	3,897	10,342
1995	2,038	701			3,396	950	4,878	11,483
1996	2,112	721	152	798	3,521	990	0	0
1997	2,113	722	1,092	2,384	3,526	993	4,682	8,492
1998	2,110	719	7,721	18,792	3,528	986	2,158	5,663
1999	2,106	715	9,102	19,145	3,537	995	13,129	17,880
2000	2,111	719	4,903	12,932	3,559	1,027	2,537	7,992
2001	2,112	726	5,269	13,579	3,556	1,011	135	538
2002	2,110	720			3,557	1,010	12,085	17,483
2003	2,110	717			3,554	1,002		

Table 8. Atlantic cod consumption (tonnes) by harp seals in NAFO zone 4Rd / 3Pn estimated using bootstrapped diet based on all years combined for each season (October-March or April-September) and annual diets.

Year	October - March				April – September			
	Average cod diet		Annual diet		Average cod diet		Annual diet	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
1990	8,197	2,269	5,373	9,166	1,777	547	6,675	3,122
1991	8,554	2,364			1,858	570	1,208	2,727
1992	8,966	2,475	2,550	5,037	1,948	599	1,292	2,930
1993	9,353	2,574	5,271	8,768	2,033	624	727	2,201
1994	9,815	2,720	484	1,281	2,131	655	1,108	2,852
1995	10,190	2,827			2,212	679	488	2,317
1996	10,569	2,958	11,751	11,276	2,292	704	717	2,015
1997	10,556	2,907	4,400	7,023	2,297	711	691	2,341
1998	10,547	2,899	10,975	11,594	2,301	707		
1999	10,508	2,891	11,326	10,635	2,303	714	3,996	5,973
2000	10,533	2,898	7,099	8,898	2,320	729		
2001	10,539	2,904	6,158	9,570	2,321	726	534	1,184
2002	10,528	2,889			2,319	729		
2003	10,530	2,880			2,320	724		

Table 9. Percent change in cod consumption resulting from a 20% decrease in model parameters.

	Parameter	Percent change
Population	Total population size	-20.0
Energy Requirements	Body Mass	-14.0
	AF	-16.5
	ME	25.0
	GF	-8.0
Residency	Proportion of all ages remaining in Arctic	5.0
	Proportion of adults remaining in Arctic	2.2
	Proportion remaining in South	-0.5
	Proportion seals in Gulf	-20.0
	Winter residency in Southern waters	-13.2
	Spring residency in Southern waters	-5.6
	Winter residency in Gulf	-17.0
	Spring residency in Gulf	-8.1
	Abundance in 4Rabc	-4.0
	Abundance in 4Rd/3Pn	-10.0
	Abundance in 4S	-6.0
Diet	Proportion cod in 4Rabc	-4.0
	Proportion cod in 4Rd/3Pn	-9.0
	Proportion cod in 4S	-6.0

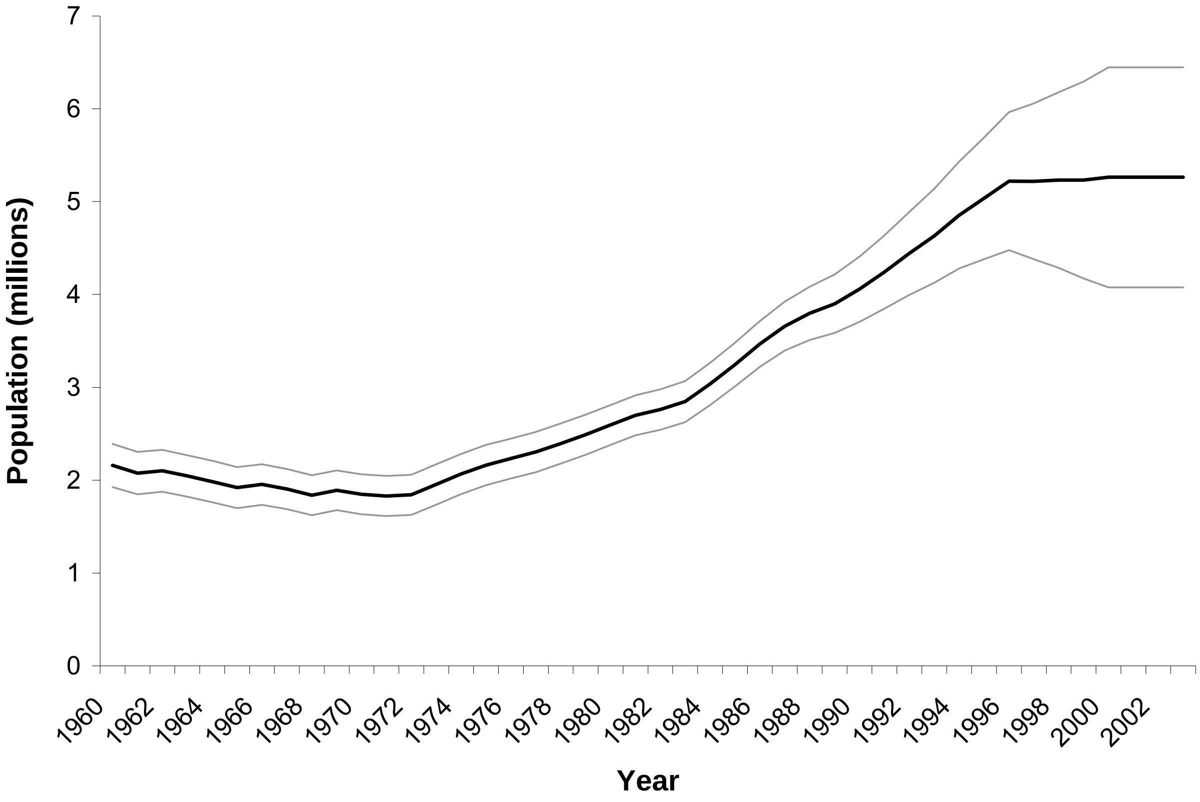

Figure 1. Harp seal (± 95% C.I.) abundance in the Northwest Atlantic.

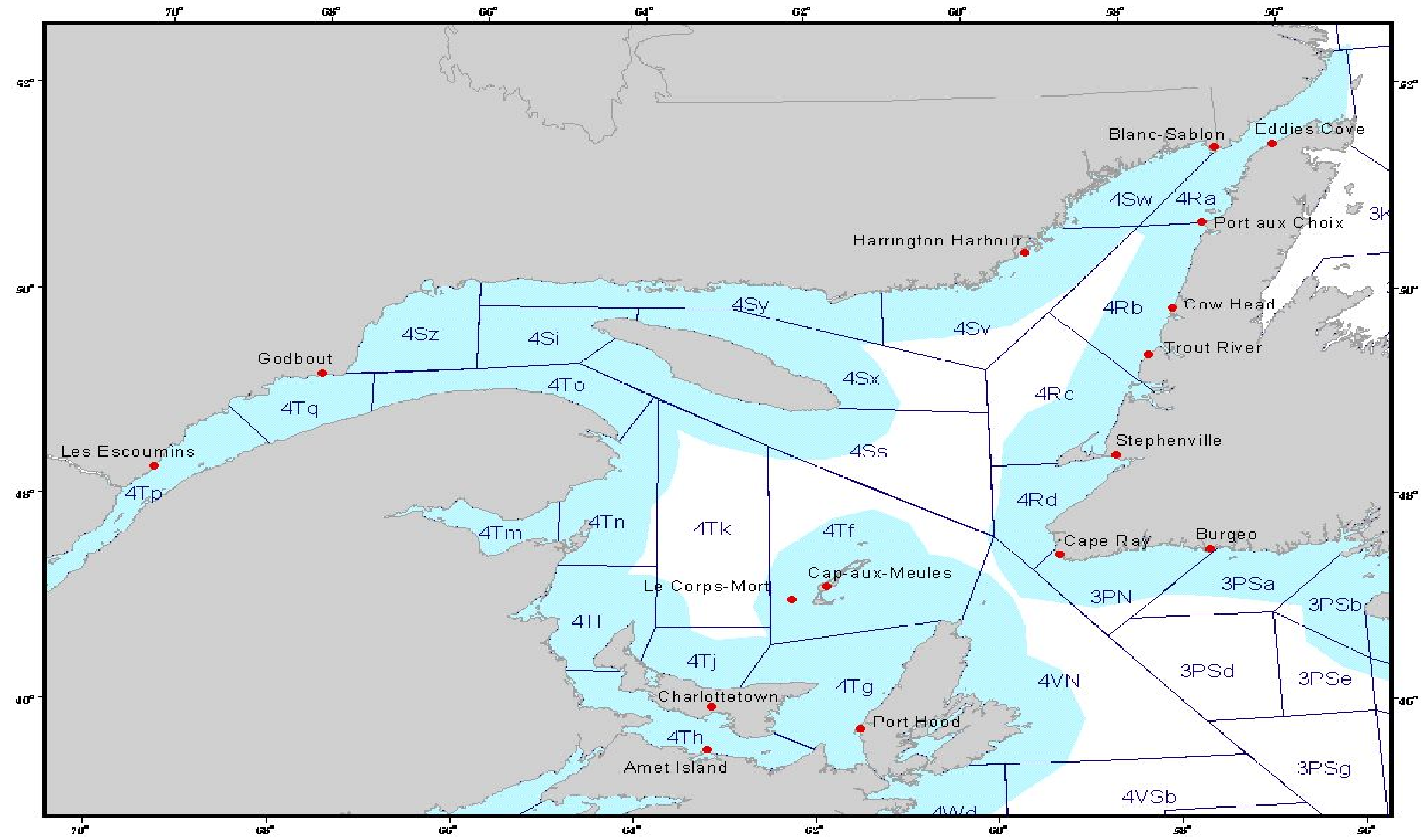

Figure 2 . NAFO fishing zones. in the Gulf of St Lawrence. Place names in 4RS3Pn show sampling locations. The shaded area shows the foraging limits likely sampled using stomach and intestine contents.

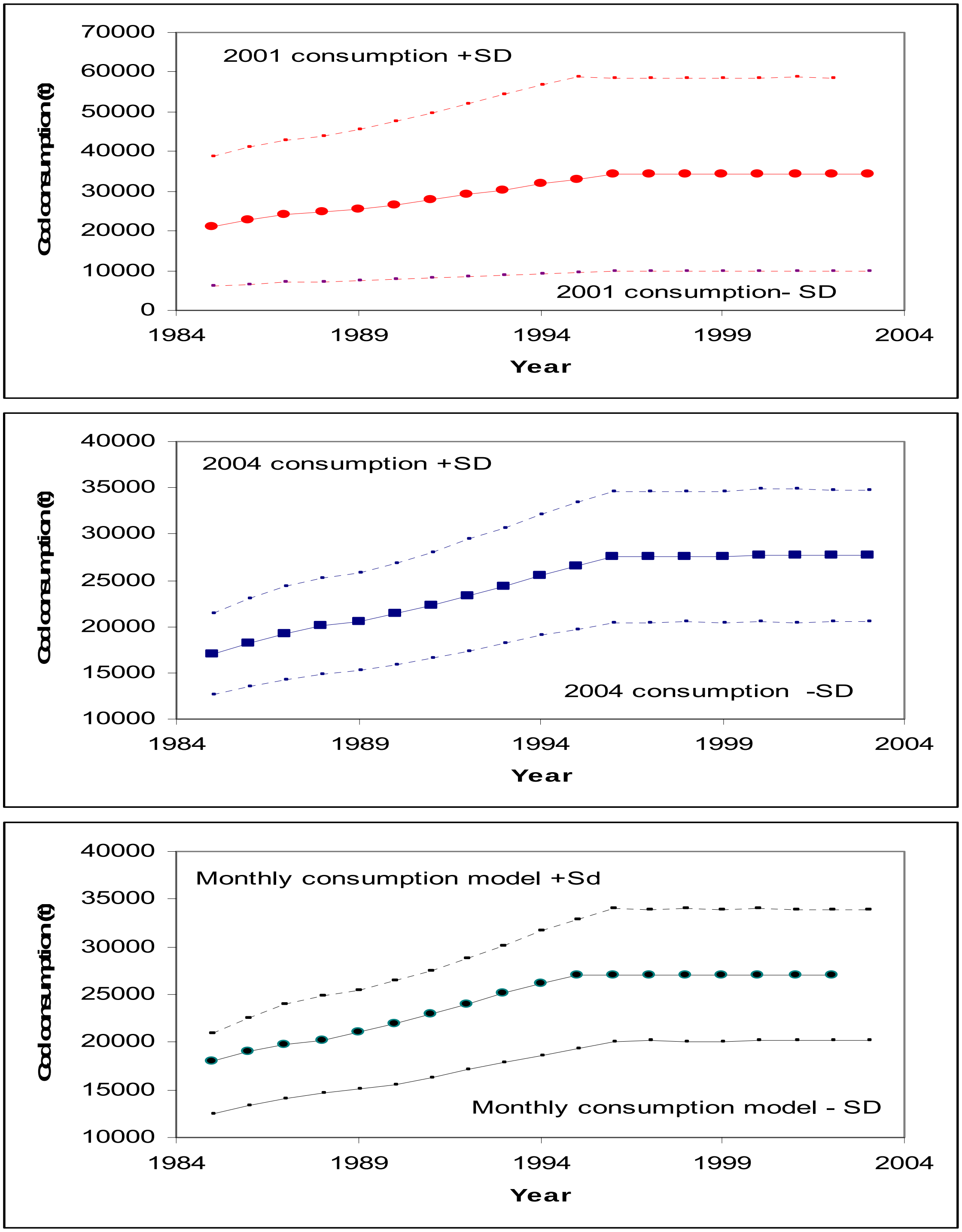

Figure 3. Estimated Atlantic cod (tonnes) consumption (Mean ± SD) by harp seals in NAFO zones 4RS obtained using the 2001 distributions and an average diet (top panel); the 2004 distributions, average body mass and average diet (middle panel) and using 2004 distributions, a monthly body mass and average diet (lower panel).

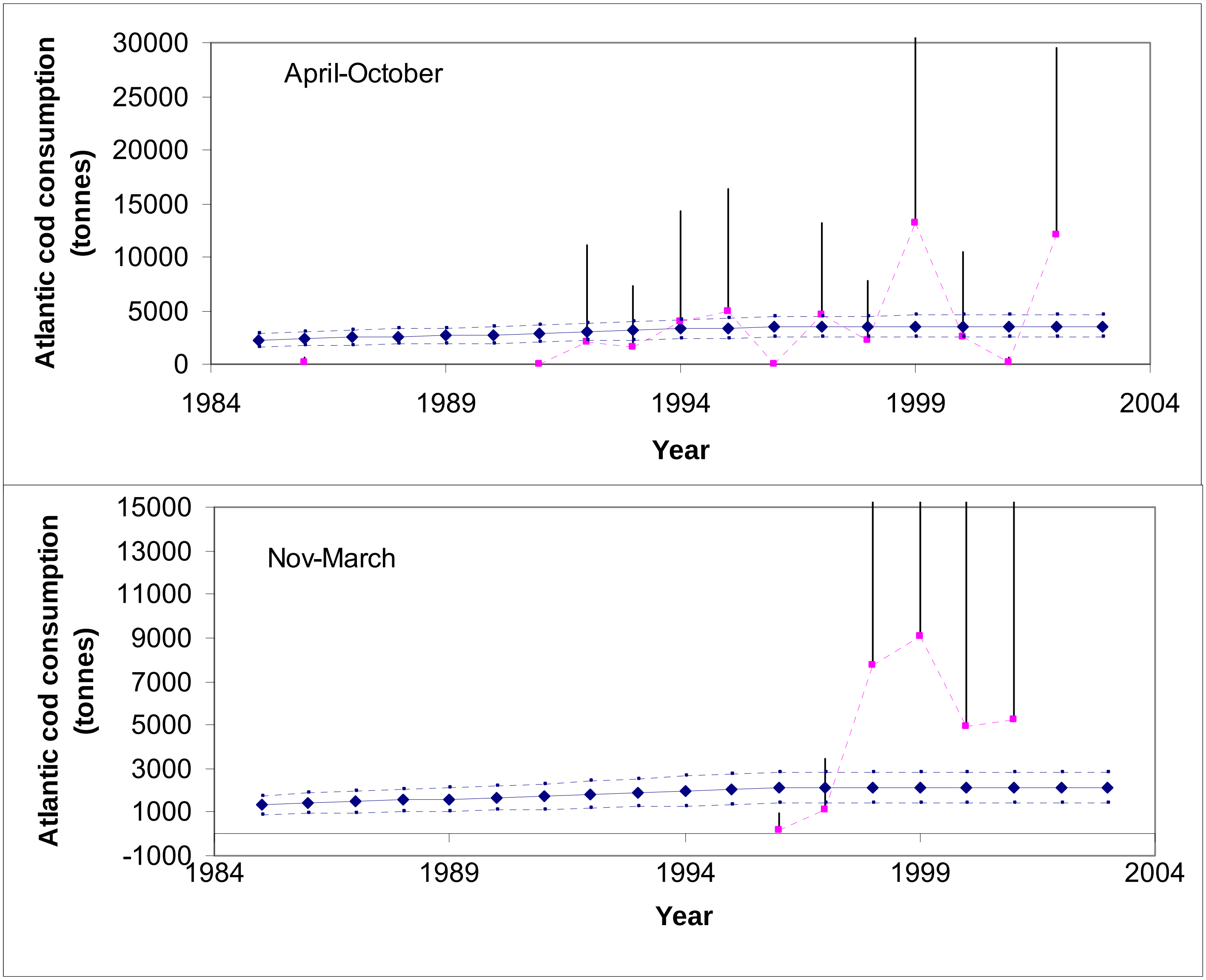

Figure 4. Estimated seasonal Atlantic cod consumption by harp seals in NAFO zone 4Rabc using an average diet based on the entire sample for the region and season (solid line) and an annual diet estimated using sample means and SD for that year's collection. For the annual diets, mean + SD are presented.

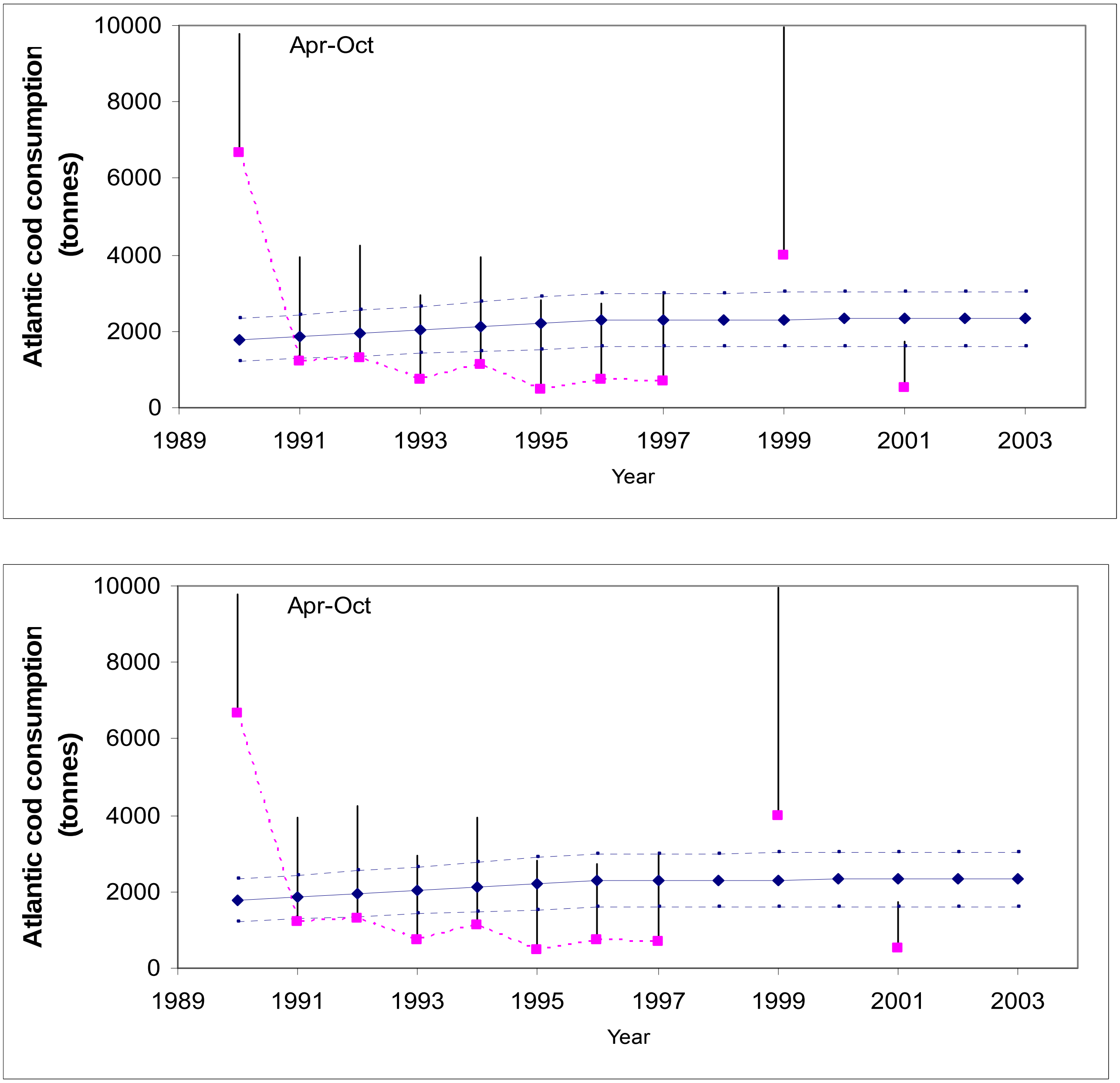

Figure 5. Estimated seasonal Atlantic cod consumption by harp seals in NAFO zone 4Rd/3Pn using an average diet based on the entire sample for the region and season (solid line) and an annual diet estimated using sample means and SD for that year's collection. For the annual diets, mean + SD are presented.