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Estimated Consumption of Atlantic cod (*Gadus morhua*), by Harp seals (*Phoca groenlandica*), in NAFO Zone 4RS

Volume estimatif de morue franche (*Gadus morhua*) consommé par le phoque du Groenland (*Phoca groenlandica*) dans les divisions 4RS de l'OPANO

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Abstract

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. Estimated consumption of 4RS Atlantic cod, in 2003 was in the order of 27,700 (SD=7,100) tonnes. Harp seals appear to feed primarily on cod less than 30 cm in length, but variability in prey length in this study and elsewhere have been observed. Overall, fifty-six percent of the estimated consumption consists of cod ≤ 3 years of age. Considerable uncertainty in the distribution of animals and diet composition at the population level affect both the magnitude and the direction of the bias in current estimates of cod consumption. These estimates differ from earlier studies by attempting to incorporate variability in estimates of population size, energy requirements, seal distribution, and diet composition.

Résumé

Nous avons estimé le volume de morue franche consommé par le phoque du Groenland dans le nord du golfe du Saint-Laurent (divisions 4RS et sous-division 3Pn de l'OPANO) de 1985 à 2003 en regroupant les données disponibles sur l'abondance de ce mammifère marin, ses besoins énergétiques, la composition de son régime alimentaire et sa répartition. Selon notre estimation, il a consommé quelque 27 700 tonnes (é.t. = 7 100) de morue franche de 4RS en 2003; il semble se nourrir surtout de morues de moins de 30 cm de longueur, mais cette longueur peut varier, comme nous l'avons observé, ainsi que d'autres chercheurs. En général, 56 % du volume consommé estimatif se compose de morues de 3 ans ou moins. L'incertitude marquée quant à la répartition du phoque du Groenland et la composition de son régime alimentaire au niveau de la population a une incidence sur l'ampleur et le sens du biais dans la présente estimation du volume de morue consommé. Notre estimation diffère de celles obtenues dans le cadre d'études antérieures du fait qu'elle tient compte de la variabilité des estimations des effectifs du phoque du Groenland, de ses besoins énergétiques, de sa répartition et de la composition de son régime alimentaire.

Introduction

Over the last 15 years 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 (Anon. 2004). This decline coincided with marked increases in seal populations throughout the region. For example harp seal biomass in the Gulf of St. Lawrence increased from 50,000 t in the 1970's to 100,000 t in the late 1990's, leading to suggestions that seals were involved in failure of the fishery (Fig. 1).

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 high compared to biomass estimates indicating that seal predation was a substantial component of the high mortality experienced by these stocks. However, owing to the large amount of uncertainty involved in the estimates the panel was reluctant to go further in evaluating impact. However, one of the panel members D. Vardy, presented a dissenting opinion (Appendix 5, pp 143-145) concluding that 'seal predation poses a serious threat to the recovery of Northern cod and other important cod stocks in Atlantic Canada and to the rebuilding of these stocks to their historical levels'.

Estimates of fish consumption by seals in Atlantic Canada have been available since the 1980's (see Hammill and Stenson 2000 and Stenson and Perry 2001 for references). These estimates were reviewed by the Eminent Panel and it was noted that estimates for the same region differ widely between studies, but it was concluded that these differences 'reflect the way in which science does and should proceed by improving techniques and obtaining more and better information' (McLaren et al. 2001).

Evaluating the magnitude of cod consumption by seals requires information on population size, energetic requirements, diet composition, size classes and energy density of the prey, as well as the distribution of marine mammal feeding effort (Harwood and Croxall, 1988; Harwood, 1992). Hammill and Stenson (2000) provided estimates of fish consumption by grey seals (*Halichoerus grypus*), harbour seals (*Phoca vitulina*), harp seals (*Phoca groenlandica*) and hooded seals (*Cystophora cristata*) throughout Atlantic Canada during the period 1990-1996. Harp seals were identified as the most important pinniped predator in the northern Gulf of St Lawrence due to the composition of their diet and abundance in this area.

Harp seals are the most abundant seal in Atlantic Canada. Abundance has increased from just under 2 million animals in Atlantic Canada in the early 1970's to just over 5 million animals in 1999 (Fig. 2). A new survey was completed during March 2004, but data are not available for the current assessment. Population modelling suggests that the population has remained stable at around 5.2 million animals (Healey and Stenson 2000; Hammill and Stenson 2003). Here we estimate fish consumption by harp seals in the northern Gulf of St Lawrence taking into account seasonal changes in feeding and variability in seal abundance, distribution, and diet composition.

Materials and Methods

Estimates of prey consumption were developed by modelling changes in population size, energy requirements, diet composition and seal distribution (see Stenson and Hammill 2004). A brief description is given below.

Harp seal abundance is monitored using aerial surveys to estimate pup production. Total population size is estimated by combining the pup production estimates with data on female reproduction rates and removals from the population from hunting and incidental catches in commercial fisheries. Changes in population size over time are monitored by fitting the model to the pup production estimates (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. 2).

Energy requirements were assumed to be constant throughout the year as in earlier presentations (Hammill and Stenson 2000, 2002) and to also vary by month. Age-specific energy requirements were calculated assuming that these could be expressed as multiples of the basic metabolic rate relationship developed by Kleiber (1975) using:

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

where GEI_i is daily gross energy intake (kjoules/day) at age i, and GP_i , the growth premium is the additional energy required at age i by young seals (< age 6). GP_i was set at 1.8, 1.6, 1.4, 1.3, 1.1, 1.1, and 1.0 for animals aged 0, 1, 2, 3, 4, 5, and ≥6 yrs respectively (Olesiuk, 1993). The activity factor (AF) was assigned a triangular function, allowing it to vary between a minimum value of 1.7, a high value of 3 and a most likely value of 2 (Worthy, 1990). BM_i is body mass at age in kg. The metabolizable energy (ME) was assigned to a uniform function with a range of 0.8 to 0.86 (Ronald *et al.,* 1984). Growth in body mass at age i (BM_i) was modeled by fitting a Gompertz growth curve to age-mass data from animals collected in Newfoundland and along the Labrador coast using Proc NLIN (SAS Institute, 1987) (Table 1)(Chabot and Stenson 2002; Chabot and Stenson unpublished data). For model simulations, where energy requirements were assumed to be constant throughout the year, body mass in April, a period when we have good sampling and animals are near their annual minimum was used in the mass at age equation above. For model simulations, where energy requirements were assumed to vary throughout the year, monthly mass at age values were used in the energy requirement equation. These values were obtained from the growth curve calculated for each month. Parameters in the growth curve were assigned as normally distributed variables in the model, using the mean and SE of each of the three parameters.

During the breeding season and the moult (March and April), nursing females and breeding males reduce their food intake, while pups derive all of their energy requirements from the female, stored reserves or feed intermittently (Sergeant 1991; Beck et al. 1993). In the constant energy model, no changes in consumption were incorporated into the model. In the variable energy model that incorporated monthly changes in body mass, food intake also varied as follows: during March, adult males, 60 % of females and all pups were assumed not to forage. All juveniles and 40% of mature females were assumed to forage. In April, when animals are moulting, all pups, and only 50% of juveniles and adult animals were assumed to forage.

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. At the end of May, the animals return to the Arctic. Annual changes in ice conditions or food availability likely affect the seasonal movements of the population (Sergeant 1991). Following Hammill and Stenson (2002), a proportion of 0.2 of all age groups were assumed to remain in the Arctic throughout the year. This was set in the model as a proportion with a uniform distribution and limits of 0.18-0.22. Some animals remain south all year round. This was also described by a uniform distribution with limits set at 0.01-0.05. A mean proportion of 0.26 (SD=.07) of the animals that came south were assumed to enter the Gulf of St. Lawrence on December 1 and remain there until May 31. This distribution is based on the average ratio of pup production in the Gulf to pup production at the Front based on aerial surveys (e.g. Stenson et al. 2003). We assumed that the proportion of juveniles entering the gulf was the same as the proportion of adults. The remainder of the population is assumed to be present in the waters off Newfoundland. The distribution of animals within the NAFO zones of the Gulf of St. Lawrence was assumed to vary by month (Fig. 3). We assumed that the proportion of the annual energy requirements obtained from different areas is proportional to the residency of the animals in the area (Table 2).

The diet of harp seals was estimated using reconstructed wet weights of stomach contents from animals collected from 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. Regression equations were obtained from published sources or stock specific relationships when available (Härkönen 1986; Benoit and Bowen 1990; Lidster *et al*. 1994; Lawson *et al*. 1995; Proust 1996). 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).

Diet samples were grouped according to location (4Rd/3Pn or 4Rabc/3Pn) (Fig. 3) and season (Winter=October-March or Spring =April-September) of collection. An average diet was calculated using all available data 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 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 and SD in the case of the annual diets.

Consumption by age class was estimated using all measured recovered cod otoliths. The proportion of each age class consumed by harp seals was estimated by multiplying the number of otoliths in each age class, by the mean weight of fish in each age class and dividing by the total mass of the complete sample. This proportion was used to partition total consumption into consumption by cod age class. Age of cod was determined using an age-length key developed from otoliths collected during the Needler research cruises of 1990-99.

The consumption model was developed as an EXCEL spreadsheet. To account for some of the variability in consumption estimates, model parameters were assigned to statistical functions using an EXCEL add-in called @Risk (Palisade Corporation Inc., Newfield, NY, USA). With @Risk, the model is 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, a mean and SD of consumption are calculated.

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 euphausids, 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 4a). In NAFO zone 4R/3Pn, there was sufficient information to divide the samples into two zones, 4Rabc and 4Rd/3Pn, and two seasons November-March and April-October. In the bootstrapped diet for 4Rabc, Atlantic herring and capelin were the two most important prey species accounting for ≥ 66% of the diet by energy, while cod accounted for ≤ 8% of the diet (Table 4a). In NAFO zone 4Rd/3Pn, Atlantic cod dominated the diet, accounting for an average of 21% of the diet during April-October and 42% of the diet during November-March. Herring and capelin were also important prey species, particularly during April-October (Table 4a). In the current analyses, the proportion of cod was lower in most regions or periods of the year compared to the 2002 assessment due in part to larger sample sizes and the inclusion of samples from Godbout, in NAFO zone 4S (Table 4b).

Consumption of cod using the 2004 diet composition and distribution of animals was about 20% lower than estimates presented in 2002. Cod consumption using the current (2004) model increased from about 17,043 tonnes (SD=4,357) in 1985 to 27,666 tonnes (SD=7,139) in 2003. Using the old (2002) model, cod consumption increased from 21,108 tonnes (SD=14,971) in 1985 to 34,223 tonnes (SD=24,331) in 2003 (Table 5; Fig. 4). Estimates of cod consumption by harp seals obtained using the constant energy budget model were essentially the same ($Mean_{2004\ constant}$=27,666 t, SD=7,139 vs $Mean_{2004\ variable}$=27,044 t, SD=6784) as estimates obtained from the model that incorporated seasonal changes in body mass and food intake (Table 5; Fig. 4).

Differences in estimated consumption between the constant energy requirement and the variable energy requirement models were less than expected. For a 12 year animal, monthly estimates of consumption estimated from the constant energy model were 753,278 kjoules and 736,600 kjoules for male and female animals respectively, resulting in an annual energy requirement of 9,039,334 kjoules for a male and 8,839,195 for a female (Fig. 5). In the variable energy model, monthly energy consumption varied from a low of 470,311 kjoules for a 12 year old male to a high of 986,881 kjoules. For a 12 year old female, energy consumption varied from a low of 452,105 kjoules to a high of 941,787 (Fig 5). Annual energy consumption estimated by the variable energy model was 8,793,293 kjoules and 9,086,835 kjoules for a 12 year old male and female respectively. Overall, estimates of annual energy consumption of the constant energy consumption and variable energy consumption models differed by less than 3%.

The proportion of cod in the diet varied considerably between years in NAFO zones 4R/3Pn (Tables 6,7). Unfortunately, suitable numbers of diet samples (n>3) are not available for NAFO zone 4S, nor for all years in NAFO zone 4R . An average diet was constructed by pooling all samples from a region and a season, and bootstrapping these diets. Consumption using these average diets was compared to consumption estimates using annual diets. Seasons were treated separately, because of differences in sample sizes (Tables 8,9; Figs. 6, 7). Throughout the time series, annual estimates of cod consumption showed considerable inter-annual variability. At the same time, consumption estimates obtained using the average diets lay within 1 SD of the annual estimates. Standard deviations of the estimates from the annual diets were quite large owing to the small sample sizes. Estimated total consumption from annual diets in NAFO zone 4R alone, varied from a low of 12,095 tonnes (SD=16,663) in 2002 to a high of 37,554 tonnes (SD=28,896) in 1999 (Table 10).

Harp seals feed primarily on small cod, but fish up to 56 cm in length were consumed (Table 11, Fig. 8). Over 74% of the cod consumed were between 16 and 31 cm long, and 90% were 10-31 cm long. However, some inter-annual variability was observed. In 1990 and 1991, harp seals fed largely on cod 13-19 cm long. In 1992, seals consumed larger fish, generally 19-28 cm in length. This tendency to feed on larger fish continued until 1996, when smaller fish once again appear in greater numbers in the diet (Fig. 9). Since 1999, fish 13-25 cm long have dominated the diet. Cod size classes were assigned to different age classes using a pooled length-age key based on all of the Needler RV data combined up to 1999 (Tables 11,12). The mean weight for each age class was estimated from the Needler cruises conducted from 1990 to 1999. Consumption of cod by age class was determined by estimating the proportion by weight that each age class contributed to the diet, then by multiplying this proportion by the annual cod consumption by harp seals (Table 13; Fig. 10). Harp seals consumed primarily small fish. Cod 0-2 years of age made up 19% of the cod consumed, while cod aged 3 years of aged composed 38% of the diet by mass, followed by cod aged 4 (24%), aged 5 (12%), and cod aged 6 and 7 combined (8%). In 2003, harp seals consumed an estimated 15,000 tonnes (SD=3,200) of cod ≤3 years of age, and consumed 11,700 tonnes (SD=2,400) of cod ≥4 years of age (Table 14, Fig. 10). Cod 6 and 7 years of age composed 13% of the total intake (2148 tonnes, SD=670).

Discussion

The principal objective of this study was to estimate cod consumption by harp seals in NAFO zone 4RS3Pn. These estimates are based on a considerable number of assumptions about population size, diet composition, spatial distribution, and energy consumption (Hammill and Stenson 2002; Stenson et al 1997; Stenson and Hammill 2004). As more information is obtained it is expected that changes will occur in these estimates.

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, changes in population size occur relatively slowly from year to year, and are relatively well known . At current harvest levels, the North Atlantic harp seal population is likely stable at around 5,200,000 animals (Healey and Stenson 2000). 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 were incorporated into the analyses, as well as seasonal changes in energy requirements. These were included by building into the model monthly changes in body mass, based on field data. Energetic costs associated with reproduction, which add about 5% to the total energy requirements of the population (Olesiuk 1993; Hammill et al. 1999 MS), were not modelled explicitly, but some of these costs will be accounted for by the monthly changes in body mass, which results from both the buildup in energy reserves and fetal growth. Energy is then expended during lactation by females and competition for mates by males, but both males and females feed very little at this time, relying instead on stored energy reserves to satisfy most of their energy needs. Neonates do not forage during the nursing period. After weaning, they forage very little, and rely on stored energy reserves during the first month of their lives.

The 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 and by others (Mohn and Bowen, 1996; Shelton *et al*., 1997). During December to May there are an estimated 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 the Eminent Panel 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 west coast of Newfoundland and absence of a seal hunting tradition in the Miquelon Islands and along the Newfoundland south coast indicates a lower abundance or an absence of animals in these areas.

Little difference in consumption was observed between the constant energy budget model, used in earlier estimates of consumption and the seasonal energy budget model (Hammill and Stenson 2002). Energy consumption in the model is driven by body mass and the different multipliers applied to the energy budget equation to account for activity and growth. Harp seals do undergo major fluctuations in body mass between late winter when adult body mass may be as high as 140 kg, or less than 100 kg near the end of the moult (Chabot and Stenson 2002; Chabot and Stenson unpublished data). In the constant energy model we used the body mass of harp seals for the month of April, when they are at their seasonal minimum.

In the seasonally variable energy model, body mass increased during fall and winter and declined during the spring as observed in the wild. This resulted in an increase in energy consumption during the fall and winter. At the same time, during the spring, breeding and moulting harp seals utilize stored energy reserves to satisfy much of their energy requirements. We incorporated this into the seasonal model by reducing consumption at this time. The effect is that overall consumption levels are similar, but the seasonal distribution of consumption changes considerably.

Overall cod consumption declined slightly from earlier assessments (Hammill and Stenson 2002). This is due in part to a reduction in the proportion of the herd occurring in NAFO zone 4R/3Pn, where the proportion of cod is very high. Also, compared to earlier assessments, the proportion of cod found in the diet has declined as more samples have been added in 4R/3Pn and from 4S. Furthermore, diet data from the Lower North Shore in 4S, were combined with data from the Godbout area, which lies at the western extremity of this zone. Samples from the latter area contain almost no cod.

In this study, we presented consumption based on an average of all diet samples collected from each area as well as estimates based on annual diets during years when sufficient data were available. In most cases standard errors between the two approaches overlapped, indicating little difference. It is tempting to prefer the annual diet approach, because it takes into account the apparent inter-annual fluctuations in the proportion of cod in harp seal diets. Large differences between the estimates obtained using an average diet and the annual diets may have resulted in part from the calculation of the proportion of cod in the diet, which would tend to exaggerate the inter-annual changes. In most cases, seal stomachs contain fewer than three prey in a stomach. As a result, stomachs tend to be dominated by one prey type. For the annual diets, the proportion of cod in the sample was taken as the average of the proportion of cod in each seal. Years with small samples, were dominated by very small amounts of cod, or very large amounts. As a result large fluctuations in the proportion of cod would be expected, along with large standard errors. In the average diet, the complete sample of diets for that season was pooled and bootstrapped. As part of the bootstrapping procedure, a sample of seal stomachs was selected, the weights of the different prey were summed and the contribution of each prey, based on the complete sample was calculated. This was repeated 1000 times, and the mean and standard error were calculated. A second reason for using the average diet is related to the manner in which the diets are reconstructed. Weight or energy contribution of each prey to the diet were reconstructed using a constant age-length-weight key and energy density data for each species, with the exception of herring and capelin energy density, which are adjusted for seasonal changes. Over time, this approach might be expected to provide a reasonable estimate of diet composition, but it fails to take into account the marked inter-annual changes in length-weight relationships that have been documented in Atlantic cod (Dutil et al. 1998). Although annual weight-length data are available for cod and some other commercial species, similar data for non-commercial species are lacking. Consequently, the diet re-constructions are limited to a general curve.

The age distribution of cod consumed by harp seals was constructed using a constant age-length-weight key. As outlined above, this approach fails to take into account inter-annual differences in weight at length that have been documented in NW Atlantic cod (Dutil et al. 1998; Stansbury et al. 1998). At the same time, it does not seem appropriate to estimate the contribution of cod to the overall diet of seals using a single curve, and then to estimate inter-annual changes in the age composition of cod consumed using annual age-length keys. Furthermore, there are some indications that age-length keys developed from harp seal stomach contents may differ considerably from age-length keys developed from research vessel data. Compared to research vessel data, harp seals may be feeding on smaller fish for a given age, than are taken in research trawls (Stansbury et al. 1998). In spite of these difficulties, the distribution of fish lengths shows that seals are concentrating on smaller cod. Overall, the preferred prey field of harp seals consists primarily of fish 10-30 cm in length. However, there is some inter-annual variability in the size spectrum of cod consumed, with seals apparently keying on larger fish in some years. Similar variability is observed elsewhere. In harp seal stomachs collected in 1998 from an inshore region in 2J3KL, 3/15 cod consumed by harp seals in a summer sample were >39 cm long, while in the winter sample from the same area and year 37/77 cod consumed were >39 cm long (Stenson and Perry 2001). These data suggest that harp seals may not just be focussing on a particular prey field size, but also select prey according to local prey abundance, which may also be linked to year class strengths.

Estimated harp seal consumption of 4RS Atlantic cod is in the order of 27,700 (SD=7,100). This total represents almost 40% of the estimated 3+ biomass of the 4RS cod stock (Anon. 2004). As outlined above, consumption may be overestimated due to uncertainties related to the distribution of animals in the Gulf, and diet composition in offshore areas. At the same time, our diet samples indicate that cod are abundant in some nearshore waters, areas poorly sampled by large boat research surveys. Furthermore, much of this consumption consists of pre-recruits or young recruits to the fishery, with 18% of this total consisting of cod 0-2 years old, and 38% consisting of age 3 cod. Removing consumption of these year classes, reduces consumption of large cod to 12,000 tonnes, or 17% of the estimated biomass. Consumption of cod by harp seals is only one source of predation mortality. Cod are also preyed upon by other cod, grey seals, hooded seals and some cetaceans such as harbour porpoise. Estimates of these other sources of mortality are needed to understand the magnitude of predation mortality, within the context of total natural mortality in order to understand role that seal predation may play in the recovery of 4RS cod.

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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. The top panel shows distribution of animals used in earlier estimates of consumption (Hammill and Stenson 2002). Bottom panel shows distribution of animals used in 2004 calculations.

NAFO	Jan	Feb	March	April	May	June	July	Aug	Sept	Oct	Nov	Dec
4Rabc	0.12	0.096	0	0.01	0.05	0.02	0.02	0.02	0.02	0.08	0.08	0.12
4Rd/3Pn	0.03	0.024	0	0.04	0.2	0.08	0.08	0.08	0.08	0.02	0.02	0.03
4S	0.2	0.15	0.2	0.20	0.25	0.45	0.45	0.45	0.45	0.45	0.45	0.2
4T	0.5	0.58	0.7	0.65	0.35	0.4	0.4	0.4	0.4	0.4	0.4	0.5
4Vn	0.05	0.05	0.05	0.05	0.05	0	0	0	0	0	0	0.05
3Ps	0.1	0.1	0.05	0.05	0.1	0.05	0.05	0.05	0.05	0.05	0.05	0.1
	1	1	1	1	1	1	1	1	1	1	1	1

	Jan	Feb	March	April	May	June	July	Aug	Sept	Oct	Nov	Dec
4Rabc	0.12	0.1	0.02	0.1	0.2	0.1	0.1	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	0.4	0.45	0.68	0.85	0.95	0.95	0.95	0.95	0.45
4T Estuary	0.25	0.2	0.15	0.2	0.1	0.1	0.05	0	0	0	0	0.25
4T South	0.1	0.29	0.55	0.25	0.15	0.1	0	0	0	0	0	0.1
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
	1	1	1	1	1	1	1	1	1	1	1	1

Table 3a. Monthly and Annual distribution of harp seal stomach samples from NAFO zone 4Rabc (Fig. 3).

Year	Jan	Feb	Mar	Apr	May	June	July	Aug	Nov	Dec	Grand Total
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

Table 3b. Monthly and Annual distribution of harp seal stomach samples from NAFO zone 4Rd/3Pn (Fig. 3).

Year	Jan	Feb	Mar	Apr	May	June	July	Aug	Nov	Dec	Grand Total
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 4a. Average diet composition of harp seals in NAFO zones 4S, 4Rabc and 4Rd/3Pn by season. Energy contribution to the diet is expressed as a proportion. Diet samples were bootstrapped 1000 times to determine mean and SD.

NAFO zone	4S		4Rabc				4Rd/3Pn			
Season			Apr-Sept		Oct-Mar		Apr-Sept		Oct-Mar	
	Ave	SD	Ave	SD	Ave	SD	Ave	SD	Ave	SD
Atlantic Cod	0.02	0.01	0.08	0.01	0.03	0.01	0.21	0.05	0.42	0.07
Atlantic Herring	0.00	0.00	0.29	0.04	0.57	0.10	0.12	0.04	0.18	0.08
Capelin	0.48	0.06	0.37	0.04	0.12	0.03	0.22	0.06	0.02	0.01
Euphausiid	0.08	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Gadoid sp.	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.01
Gadus sp.	0.04	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.01
Redfish sp.	0.00	0.00	0.00	0.00	0.00	0.00	0.08	0.04	0.20	0.04
Rock Cod	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Salmon	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Sand Lance	0.26	0.05	0.04	0.01	0.03	0.01	0.27	0.06	0.02	0.01
Other prey	0.11		0.19		0.25		0.09		0.12	

Table 4b. Average diet composition used during 2002 cod stock assessment. Average diet composition of harp seals in NAFO zones 4S, 4Rabc and 4Rd/3Pn by season used in 2002 cod stock assessment (Hammill and Stenson 2002). Energy contribution to the diet is expressed as a proportion. Diet samples were bootstrapped 1000 times to determine mean and SD.

NAFO zone	4Rabc				4Rd/3Pn				4S	
Season	Apr-Sept		Oct-Mar		Apr-Sept		Oct-Mar		Apr-Mar	
	Ave	SD	Ave	SD	Ave	SD	Ave	SD	Ave	SD
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	0.000	0.000	0.000	0.000	0.002	0.002	0.080	0.027
Gadoid sp.	0.000	0.000	0.000	0.000	0.000	0.000	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.	0.000	0.000	0.000	0.000	0.083	0.044	0.203	0.042	0.000	0.000
Rock Cod	0.010	0.003	0.000	0.000	0.000	0.000	0.003	0.002	0.000	0.000
Salmon	0.005	0.004	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
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	

Table 5. Cod consumption (tonnes) using diet and distributions from 2002 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	21108	14971	17043	4357	16742	4251
1986	22682	16075	18249	4703	17962	4608
1987	24002	16986	19291	4990	19017	4900
1988	24942	17706	20025	5171	19724	5070
1989	25614	18185	20546	5299	20220	5194
1990	26599	18854	21363	5490	21003	5398
1991	27791	19714	22310	5698	21924	5592
1992	29101	20655	23388	6016	22979	5840
1993	30358	21538	24389	6244	23993	6165
1994	31847	22568	25580	6574	25165	6506
1995	33093	23558	26537	6828	26118	6738
1996	34292	24429	27522	7092	27082	6966
1997	34241	24322	27522	7109	27048	6888
1998	34245	24277	27552	7076	27072	7011
1999	34150	24300	27530	7080	26988	6870
2000	34218	24239	27674	7176	27072	6895
2001	34249	24367	27687	7244	27039	6857
2002	34311	24451	27649	7120	27049	6868
2003	34223	24331	27666	7139	27044	6784

Table 6. Number of stomachs (n), mean proportion and standard deviation (SD) of cod in annual diet samples from NAFO zone 4Rd/3Pn. Years with less than 4 stomachs are not included in the average of the annual samples. The annual average has been calculated from the mean of the 10 years. The bootstrap mean was calculated by combining all stomachs from all years, including years with less than four stomachs and bootstrapping this large sample.

Year	n	Cod	SD	n	Cod	SD
		April-Sept.			Oct-March	
1989	2	0		2	0.926	
1990	4	.788	.319	10	.278	.449
1991	21	.136	.306			
1992	23	.137	.308	15	.112	.223
1993	40	.075	.221	9	.236	.373
1994	50	.110	.270	7	.020	.052
1995	17	.052	.216	3	.333	.577
1996	27	.066	.182	35	.462	.417
1997	31	.06	.209	17	.174	.267
1998	0			21	.437	.442
1999	4	0	0	22	.452	.407
2000	2	.372	.527	39	.282	.338
2001	4	.052	.104	16	.248	.375
Ave. annual samples	10	.185	.232	10	.270	.148
Average from bootstrap all samples	209	.210	.045	191	.417	.065

Table 7. Number of stomachs (n), mean proportion and standard deviation (SD) of cod in annual diet samples from NAFO zone 4Rabc. Years with less than 4 stomachs are not included in the average of the annual samples. The annual average has been calculated from the mean of the annual diets. The bootstrap mean was calculated by combining all stomachs from all years, including years with less than four stomachs and bootstrapping this large sample.

Year	n	Cod	SD	n	Cod	SD
	April-Sept.			Oct.-March		
1986	5	.007	.015			
1989	3	0	0			
1990	3	0	0			
1991	5	0	0			
1992	18	.054	.231			
1993	41	.043	.149			
1994	18	.093	.251			
1995	14	.115	.273			
1996	5	0	0	39	.002	.010
1997	10	.106	.190	27	.014	.029
1998	14	.049	.126	27	.099	.231
1999	6	.298	.394	28	.117	.237
2000	9	.059	.176	25	.063	158
2001	13	.003	.012	30	.07	.167
2002	13	.274	.381			
Ave. Annual diets	13	.085	.098	6	.061	.046
Average from Bootstrap	179	.081	.013	177	.027	.006

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 (Nov-March or Apr-Oct) and an annual diet.

Year	Average cod diet 4Rd/3Pn Nov-March		Annual diet 4Rd/3Pn Nov-March		Average cod diet 4Rd/3Pn Apr-Oct		Annual diet 4Rd/3Pn Apr-Oct	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
1985								
1986								
1987								
1988								
1989								
1990	8197	2269	5373	9166	1777	547	6675	3122
1991	8554	2364			1858	570	1208	2727
1992	8966	2475	2550	5037	1948	599	1292	2930
1993	9353	2574	5271	8768	2033	624	727	2201
1994	9815	2720	484	1281	2131	655	1108	2852
1995	10190	2827			2212	679	488	2317
1996	10569	2958	11751	11276	2292	704	717	2015
1997	10556	2907	4400	7023	2297	711	691	2341
1998	10547	2899	10975	11594	2301	707		
1999	10508	2891	11326	10635	2303	714	3996	5973
2000	10533	2898	7099	8898	2320	729		
2001	10539	2904	6158	9570	2321	726	534	1184
2002	10528	2889			2319	729		
2003	10530	2880			2320	724		

Table 9. Atlantic cod consumption (tonnes) by harp seals in NAFO zone 4Rabc estimated using bootstrapped diet based on all years combined for each season (Nov-March or Apr-Oct) and an annual diet.

Year	Average cod diet 4Rabc Nov-March		Annual diet 4Rabc Nov-March		Average cod diet 4Rabc Apr-Oct		Annual diet 4Rabc Apr-Oct	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
1985	1304	445			2183	604		
1986	1400	479			2332	647	201	449
1987	1483	509			2462	683		
1988	1539	528			2554	711		
1989	1579	541			2622	731		
1990	1638	558			2727	758		
1991	1711	585			2852	799	0	0
1992	1793	611			2991	836	2010	9066
1993	1871	641			3118	864	1587	5730
1994	1963	673			3271	914	3897	10342
1995	2038	701			3396	950	4878	11483
1996	2112	721	152	798	3521	990	0	0
1997	2113	722	1092	2384	3526	993	4682	8492
1998	2110	719	7721	18792	3528	986	2158	5663
1999	2106	715	9102	19145	3537	995	13129	17880
2000	2111	719	4903	12932	3559	1027	2537	7992
2001	2112	726	5269	13579	3556	1011	135	538
2002	2110	720			3557	1010	12085	17483
2003	2110	717			3554	1002		

Table 10. Total cod consumption (tonnes) by harp seals in NAFO zone 4R estimated from annual diets only.

Year	Total	SD
1996	12620	11483
1997	10865	11515
1999	37554	28896
2001	12095	16663

Table 11. Number of cod found in each size class per year, where size class 7 is all fish 6-8 cm long.

Year Size class	7	10	13	16	19	22	25	28	31	34	37	40	43	46	49	52	55	Total
1986				1		1	3	1										6
1987				1														1
1989									2									2
1990		18	27	15	10	5	9	1	5	2	2	1		1				96
1991	1	5	2	6	8	2	1											25
1992		4	14	3	10	4	11	5	1			2		1				55
1993		2		1	4	4	8	6	8	2	2	1	1	1	1			41
1994		1			3	2		1	2	2	1						1	13
1995		1		1	3	1	1				1							8
1996		4	9	18	47	28	16	5	11	5	12	16	3	2	1	1		178
1997	1	9	16	19	13	17	10	9		1	5			2				102
1998		10	12	10	22	7	9	1		1								72
1999		7	32	22	17	19	13	6	5	3	3			1				128
2000		4	21	14	24	25	7	10	8	7			1					121
2001		0	1	2	4	7	11	6	5	2		1						39
2002		0	3	3	5	3	3	0										17
																		0
Total	2	65	137	116	170	125	102	51	47	25	26	21	5	8	2	1	1	904

Table 12. Age-Length key

Age classes developed from grouped Needler data

	Age Class	0	1	2	3	4	5	6	7
Size Class	#Otoliths								
7	2	1	1						
10	54	43	9	2	2				
13	80		61	19					
16	75		13	60	2				
19	120		1	72	47				
22	71			26	44	1			
25	68			14	49	5			
28	29			2	19	8	0		
31	29			0	13	15	1		
34	13				3	9	2		
37	23				1	14	7	1	
40	20				0	8	10	1	
43	4					1	2	1	
46	7						3	3	1
49	2						1	1	
52	1							1	
55	1								1
	Total	44	84	194	180	60	25	8	2

Table 13. Weights at age (kg) for cod aged 0 to 7. Age 1-7 from Needler cruises, age 0 from Banville (2003)

ÂGE	0	1	2	3	4	5	6	7
1990	0.00509	0.027	0.128	0.268	0.478	0.798	1.161	1.323
1991	0.00509	0.013	0.128	0.254	0.445	0.749	1.013	1.487
1992	0.00509	0.020	0.118	0.266	0.521	0.784	1.068	1.117
1993	0.00509	0.020	0.126	0.274	0.471	0.728	0.988	1.406
1994	0.00509	0.024	0.090	0.292	0.510	0.748	1.013	1.304
1995	0.00509	0.058	0.151	0.285	0.600	0.788	1.130	1.198
1996	0.00509	0.058	0.158	0.308	0.593	0.880	1.070	1.354
1997	0.00509	0.041	0.141	0.343	0.674	1.024	1.220	1.411
1998	0.00509	0.061	0.146	0.368	0.626	0.997	1.249	1.349
1999	0.00509	0.069	0.174	0.334	0.643	0.933	1.312	1.682
Mean	0.00509	0.039202	0.135981	0.299235	0.555968	0.842859	1.122321	1.363062
SD	0	0.020911	0.023317	0.037853	0.080781	0.108237	0.110741	0.154239

Table 14. Biomass (tonnes) by age class of cod consumed by harp seals in 4RS, estimated from the average total biomass (2004 variable energy intake model; Table 6), number of cod found in different size classes (Table 10), age-length key (Table 11), and mean body mass of cod at age (Table 12).

	Age 0		Age 1		Age 2		Age 3		Age 4		Age 5		Age 6		Age 7	
	Ave	SD	Ave	SD	Ave	SD	Ave	SD	Ave	SD	Ave	SD	Ave	SD	Ave	SD
1985	22	10	373	340	2743	1036	6333	1705	3971	1100	1972	905	940	359	388	200
1986	23	11	413	382	2928	1094	6803	1876	4261	1193	2089	909	1006	383	414	211
1987	24	11	425	380	3105	1189	7207	1990	4512	1279	2227	1018	1068	405	439	224
1988	25	12	454	413	3230	1233	7464	2031	4690	1365	2292	1007	1108	427	456	237
1989	26	12	452	416	3298	1218	7681	2196	4799	1341	2365	1060	1135	442	468	249
1990	27	12	470	428	3446	1368	7965	2219	4973	1371	2443	1059	1183	454	484	246
1991	28	13	493	454	3593	1374	8321	2303	5212	1506	2551	1107	1232	476	511	273
1992	30	14	519	465	3765	1437	8711	2424	5454	1514	2702	1254	1289	480	535	282
1993	31	14	539	497	3929	1504	9089	2542	5703	1641	2818	1294	1343	500	553	280
1994	32	15	570	513	4106	1591	9545	2686	5973	1706	2946	1322	1408	533	581	304
1995	34	16	588	532	4264	1643	9894	2757	6197	1756	3074	1394	1472	586	605	319
1996	35	16	609	569	4467	1813	10256	2805	6420	1811	3173	1426	1517	563	623	315
1997	35	16	614	571	4442	1722	10273	2894	6414	1765	3177	1428	1520	587	622	309
1998	35	16	613	563	4426	1705	10290	2952	6418	1815	3194	1461	1520	587	631	331
1999	35	16	605	529	4380	1574	10250	2888	6403	1792	3151	1426	1511	567	623	318
2000	35	15	607	537	4429	1671	10242	2750	6425	1812	3163	1373	1512	554	629	334
2001	34	15	613	566	4410	1610	10235	2773	6421	1781	3155	1405	1520	589	623	322
2002	35	16	608	537	4408	1678	10248	2797	6424	1826	3153	1387	1515	568	621	313
2003	35	16	608	568	4393	1588	10242	2755	6428	1800	3174	1441	1527	592	621	314

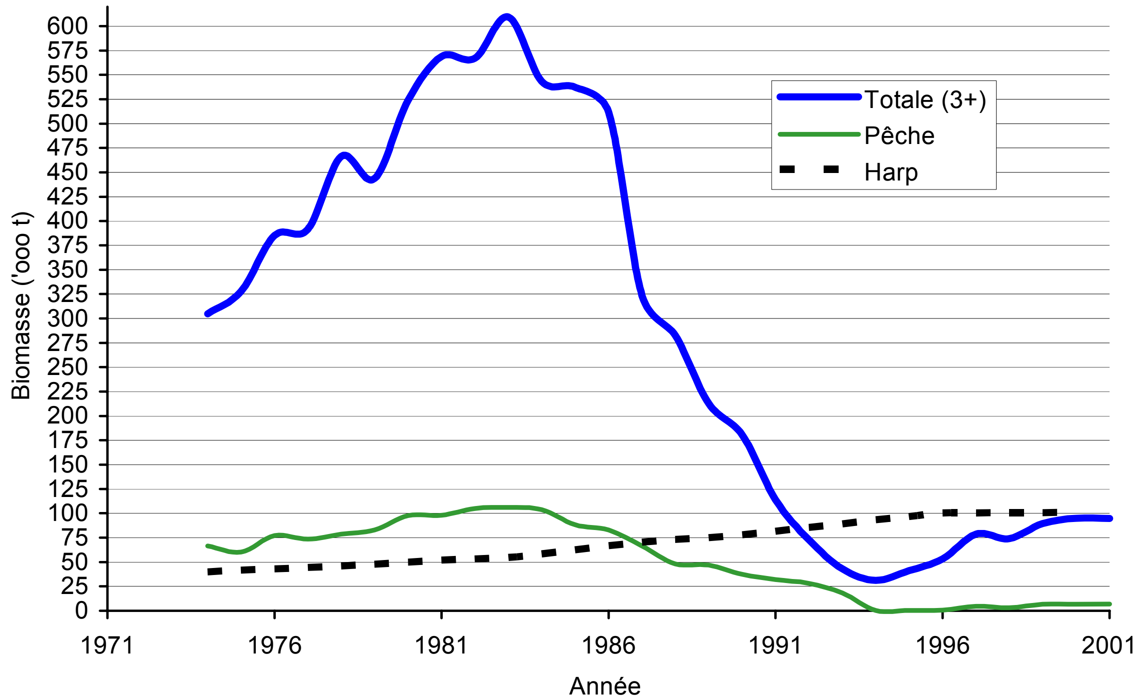


Figure 1. Cod, harp seal and grey seal biomass and cod landings in zone 4RS. Cod data are from Frechet (DFO, unpublished). Seal biomass data are from Hammill and Stenson (unpublished data)

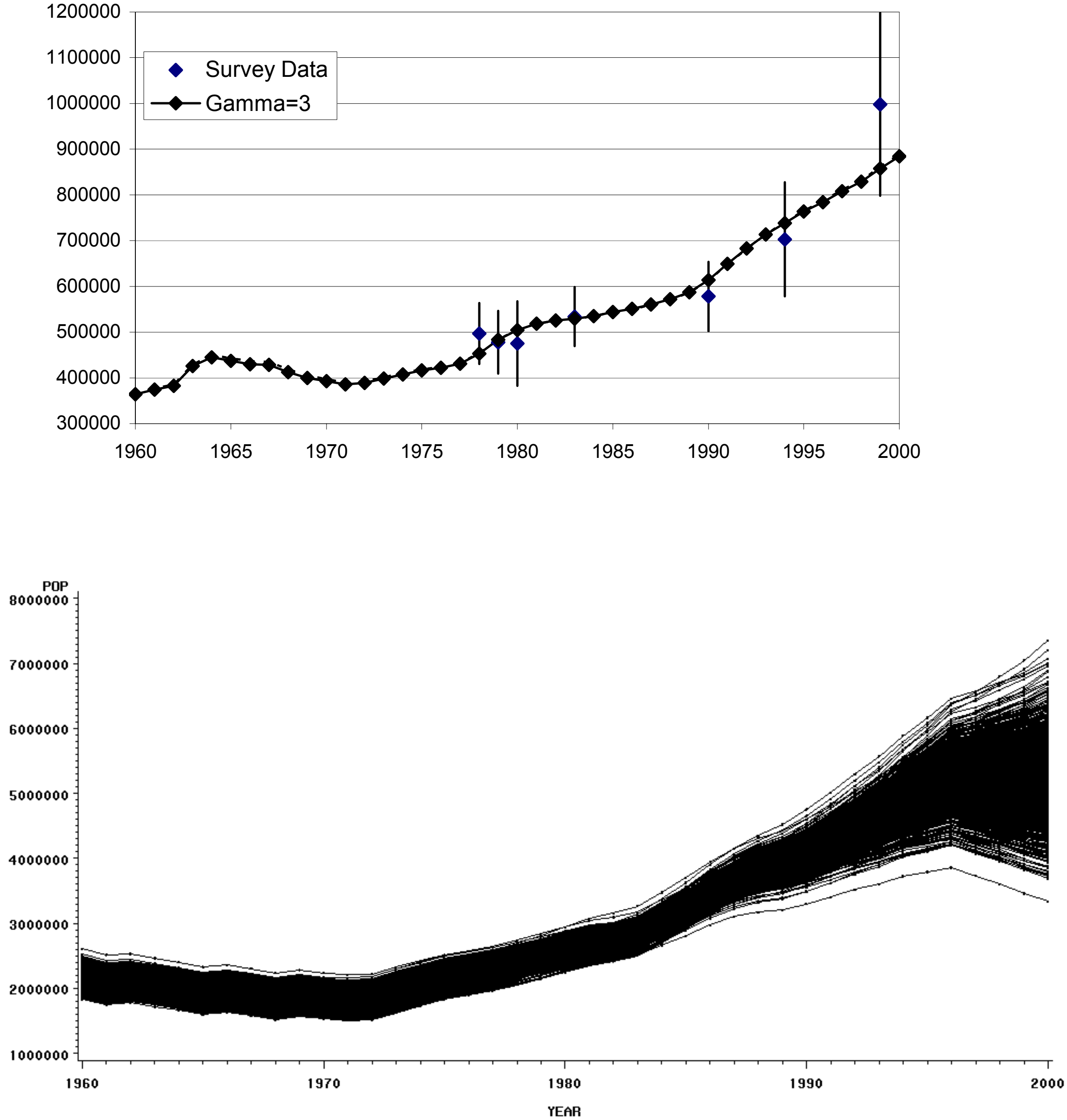


Figure 2. Harp seal abundance in Atlantic Canada. Top panel shows estimated trajectory of pup production, assuming pup mortality rates are three times adult mortality rates. Point estimates (with error bars) are survey estimates. Changes in total population size (bottom panel) obtained by resampling 1000 times from the distribution of pup production estimates (Healey and Stenson 2000).

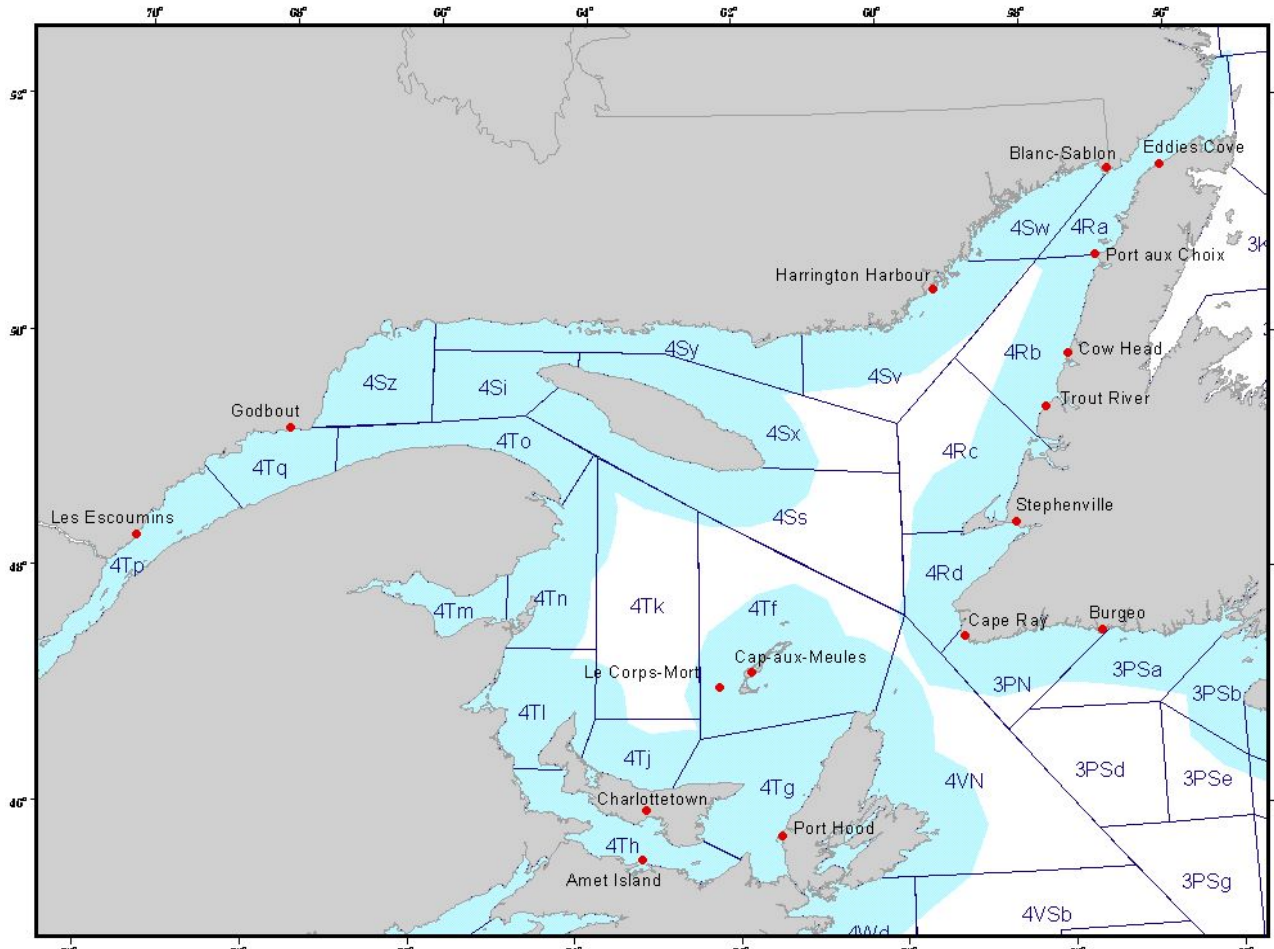


Figure 3. NAFO fishing zones in the Gulf of St Lawrence. Place names in 4RS3Pn show sampling locations. The shaded area shows the foraging limits likely sampled using stomach and intestine contents.

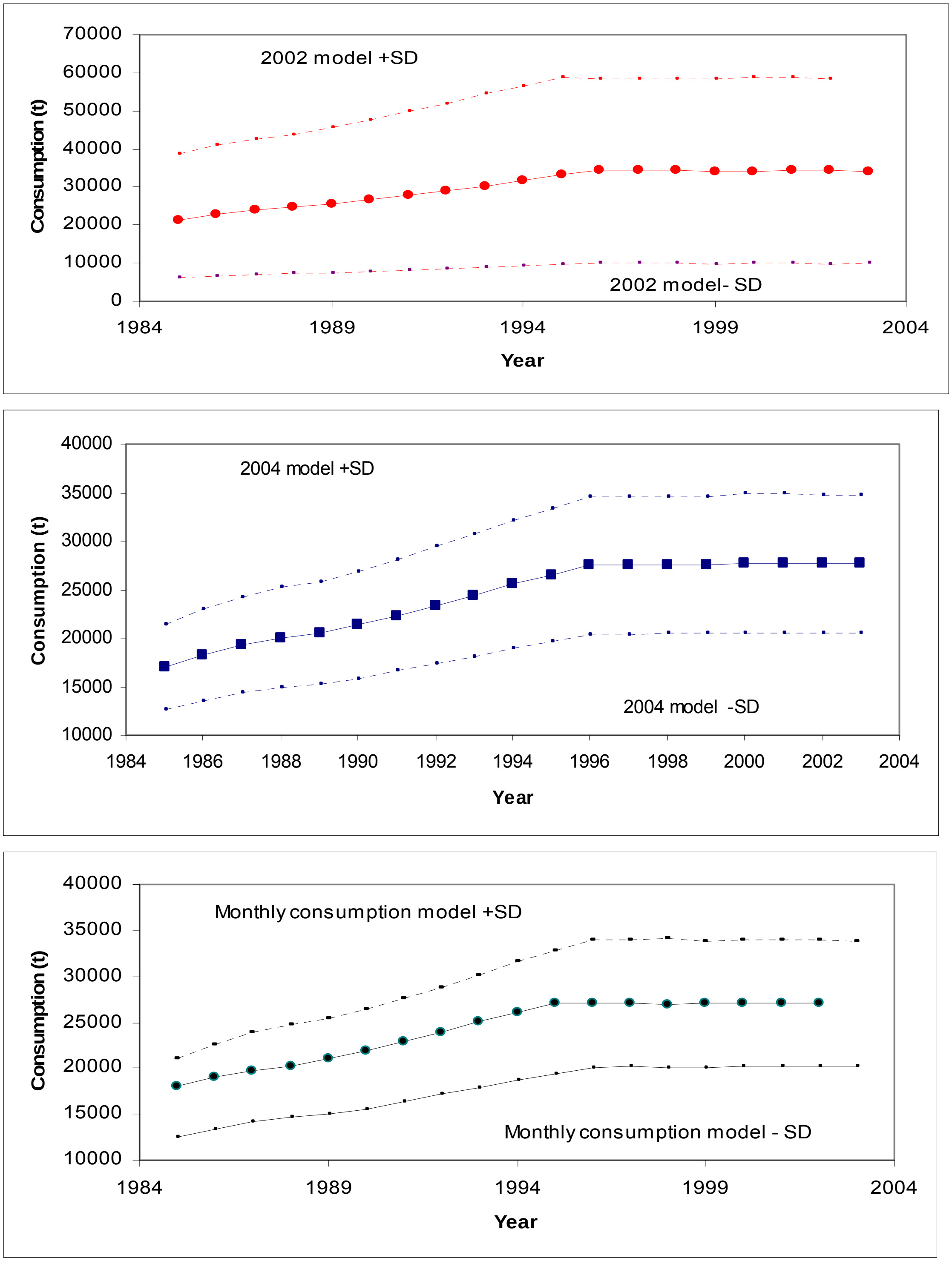
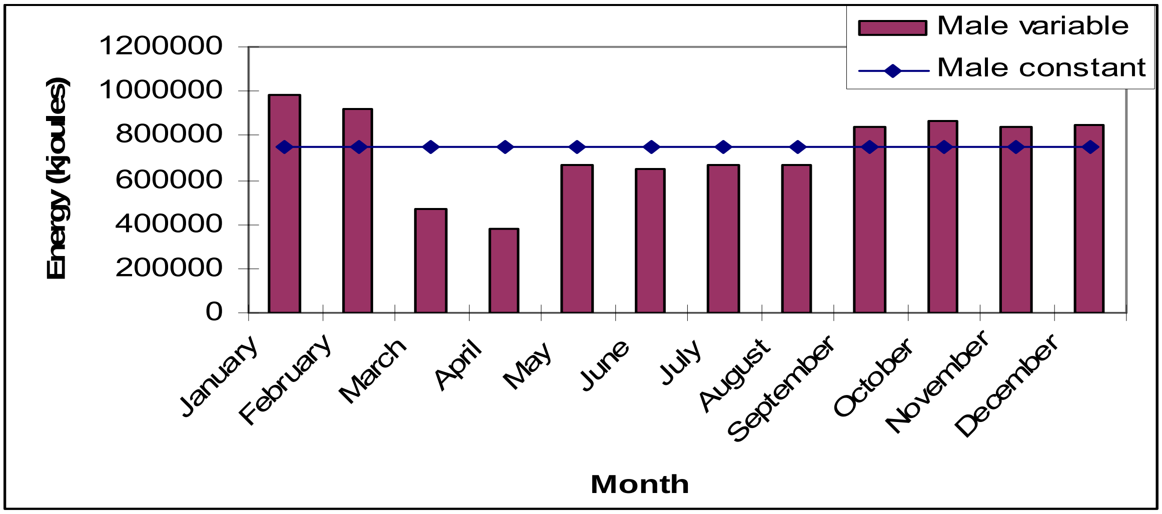


Figure 4. Estimated Atlantic cod (tonnes) consumption (Mean ± SD) by harp seals in NAFO zones 4RS obtained using a constant energy requirement, the 2002 distributions (Hammill and Stenson 2002) and an average bootstrapped diet (top panel); using the 2004 distributions, a constant energy budget and an average bootstrapped diet (middle panel) and using 2004 distributions, monthly changes in energy requirements and an average diet.



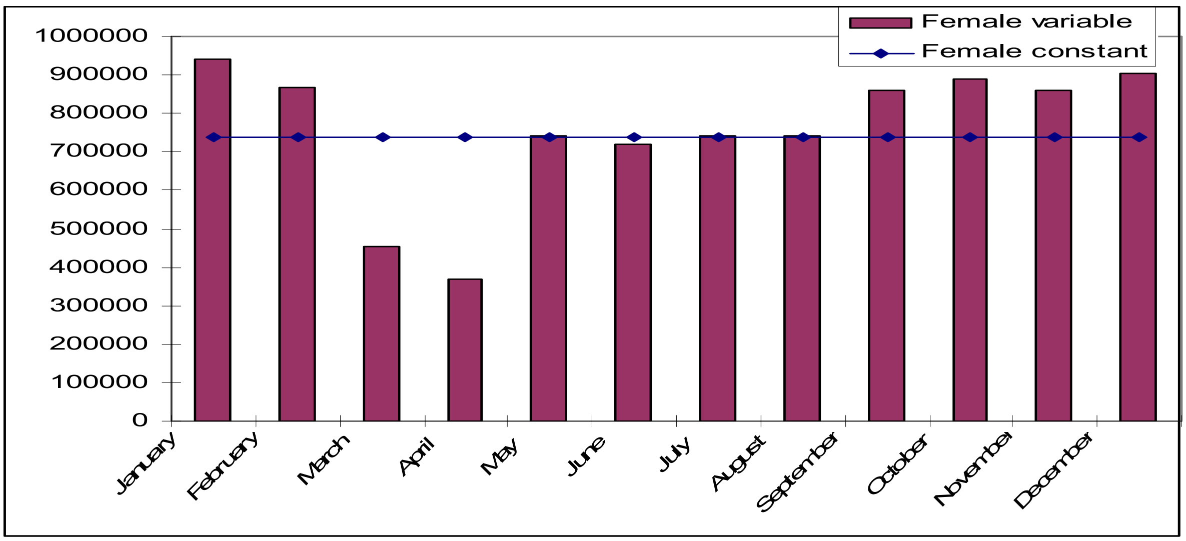


Figure 5. Monthly estimates of energy consumption for a 12 year old male (top) and a 12 year old female (bottom) estimated using a constant energy and a variable energy requirement model.

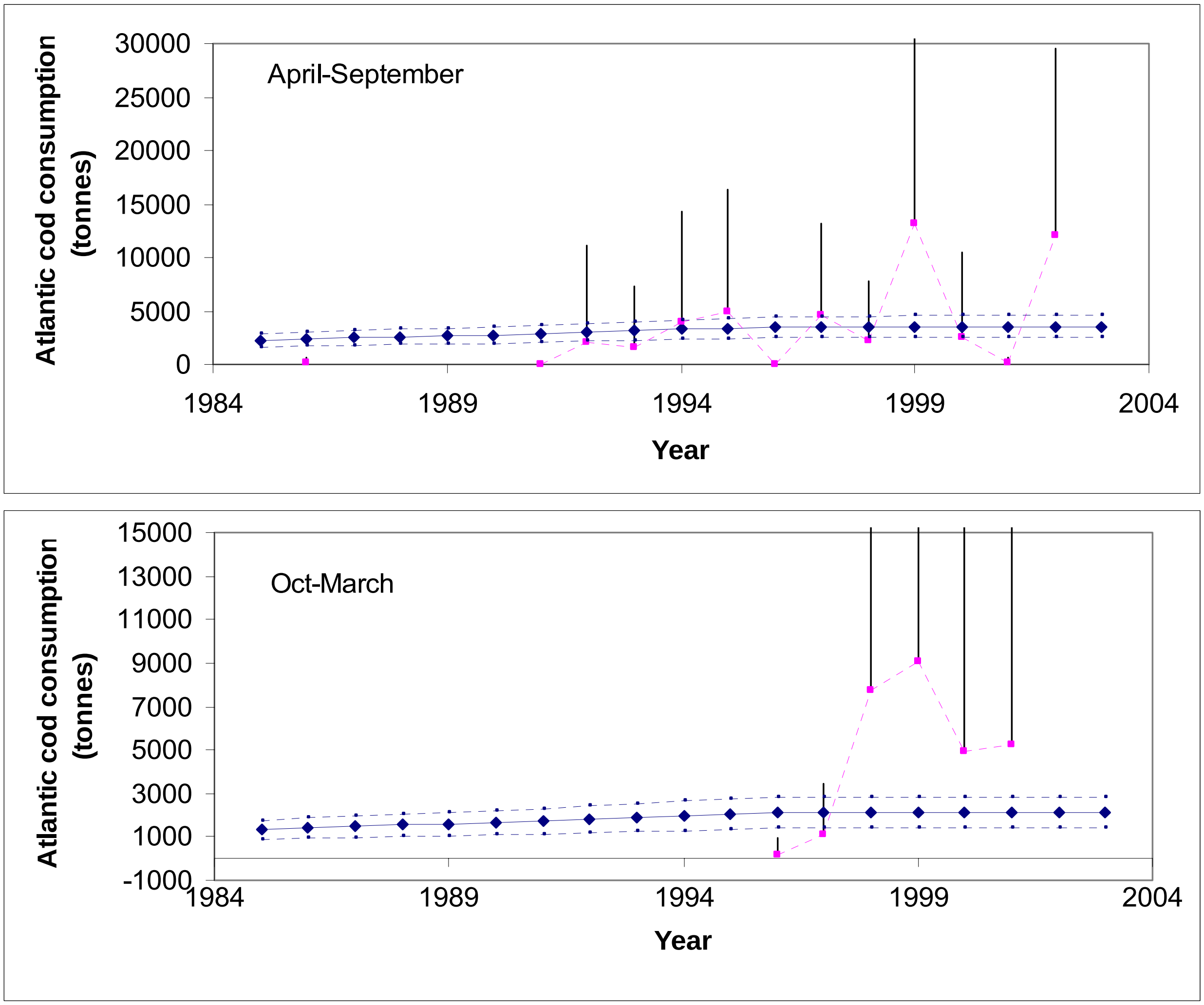


Figure 6. Estimated seasonal Atlantic cod consumption by harp seals in NAFO zone 4Rabc using an average diet based on the entire sample for the region and the season and an annual diet estimated using sample means and SD for that year's collection. For the annual diets, mean (+ 1 SD) are presented.

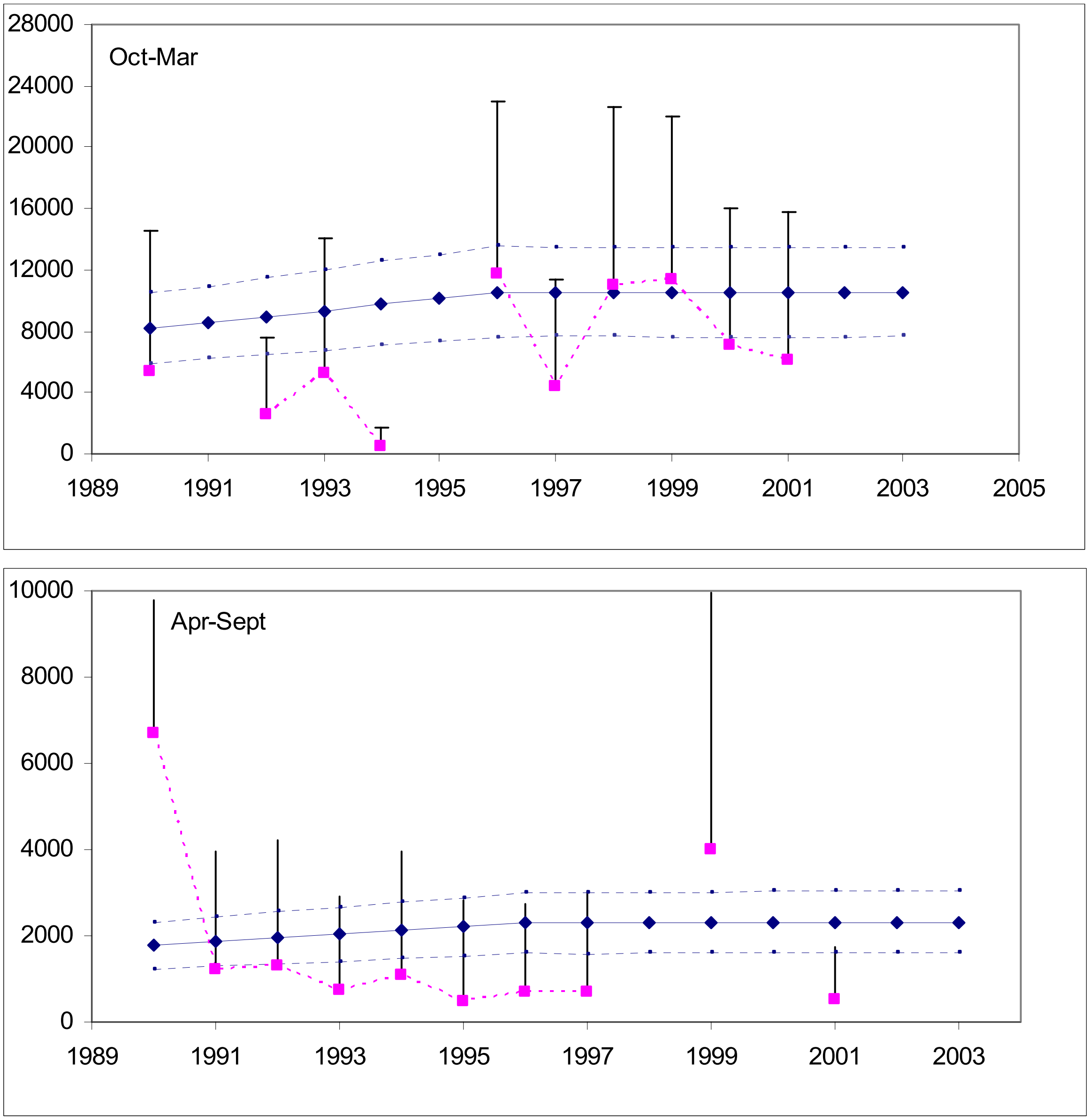


Figure 7. Estimated seasonal Atlantic cod consumption by harp seals in NAFO zone 4Rd/3Pn using an average diet based on the entire sample for the region and an annual diet estimated using sample means and SD for that year's collection. For the annual diets, mean and mean + Sd are presented.

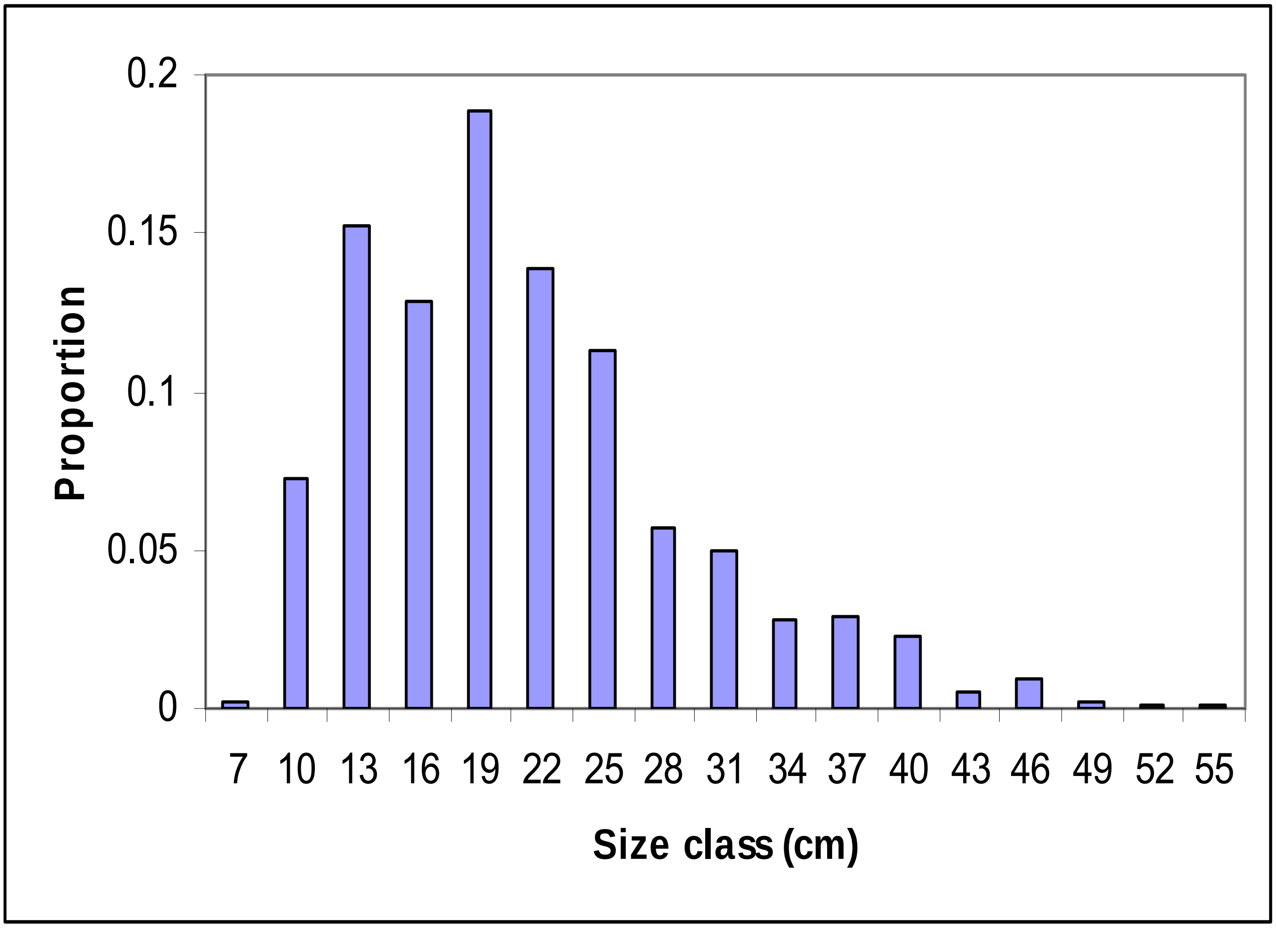
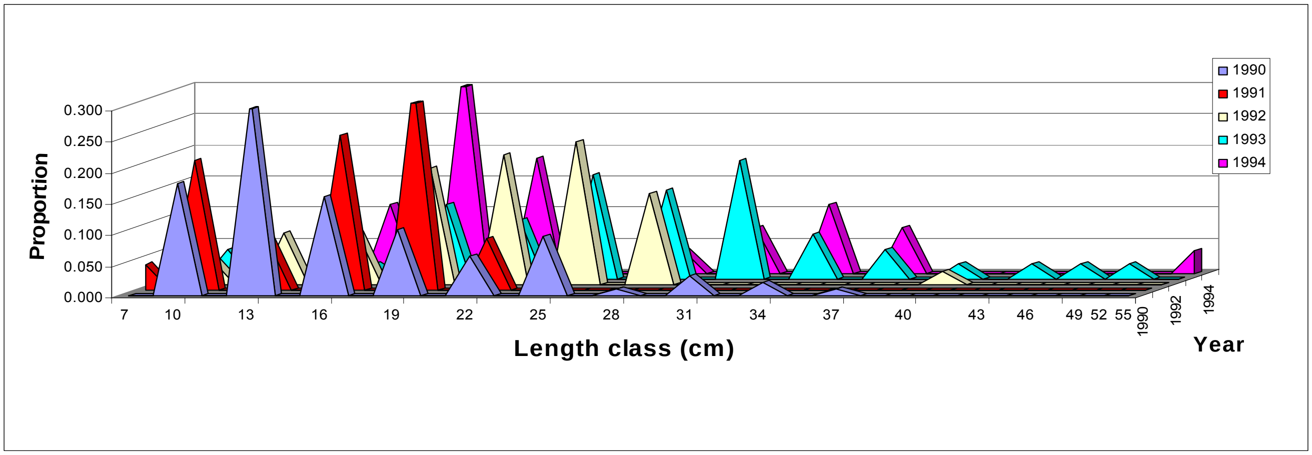
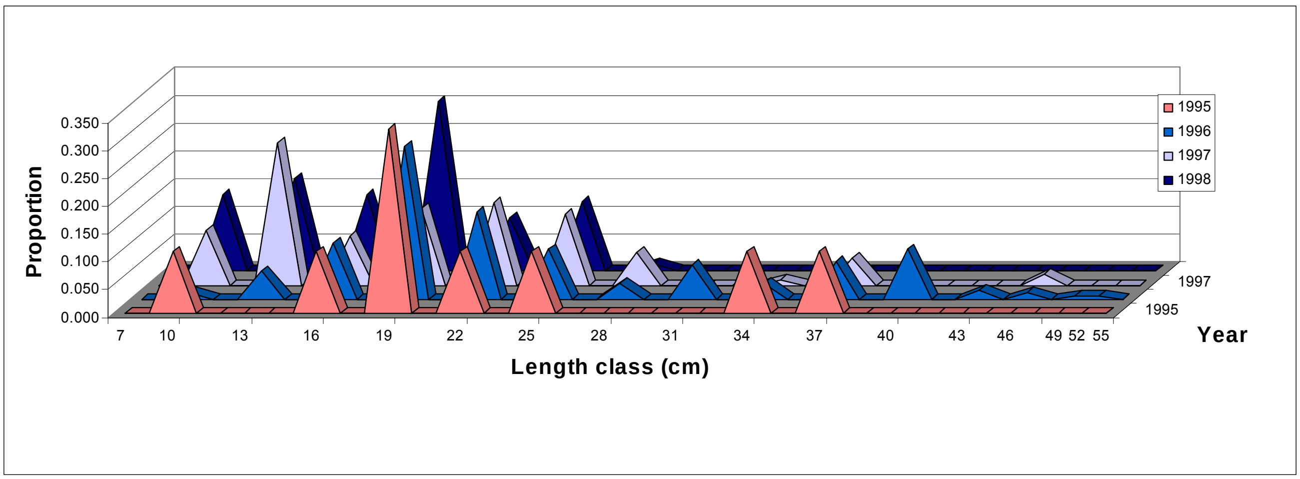


Figure 8. Reconstructed length (cm) frequency distribution of cod found in harp seal stomachs collected in NAFO zone 4R/3Pn.





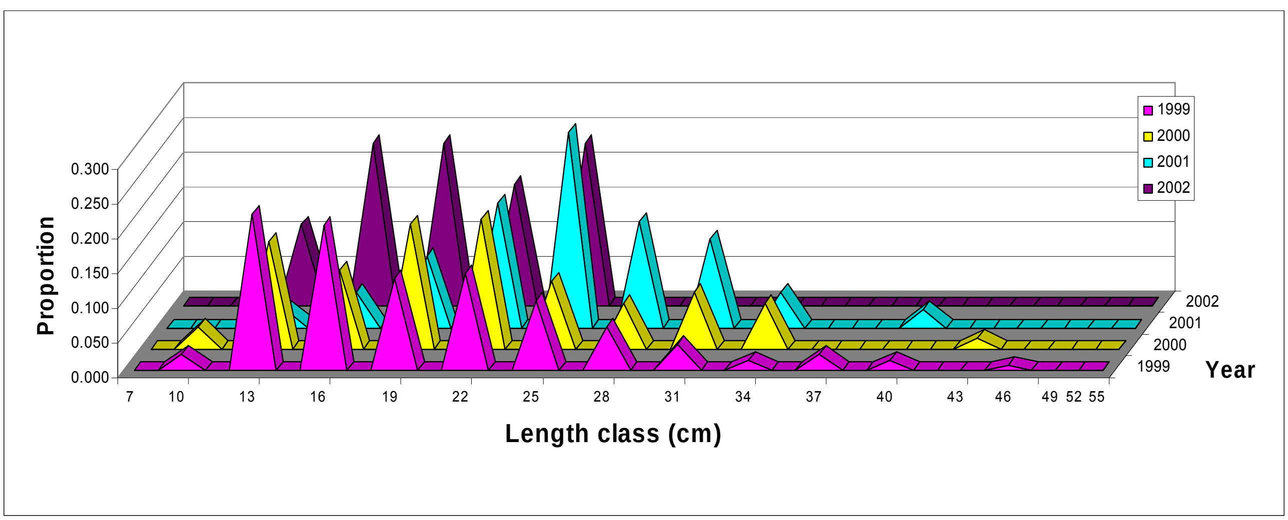


Figure 9. Distribution of size classes of 904 cod consumed in the northern Gulf of St. Lawrence by harp seals between 1990 and 2002.

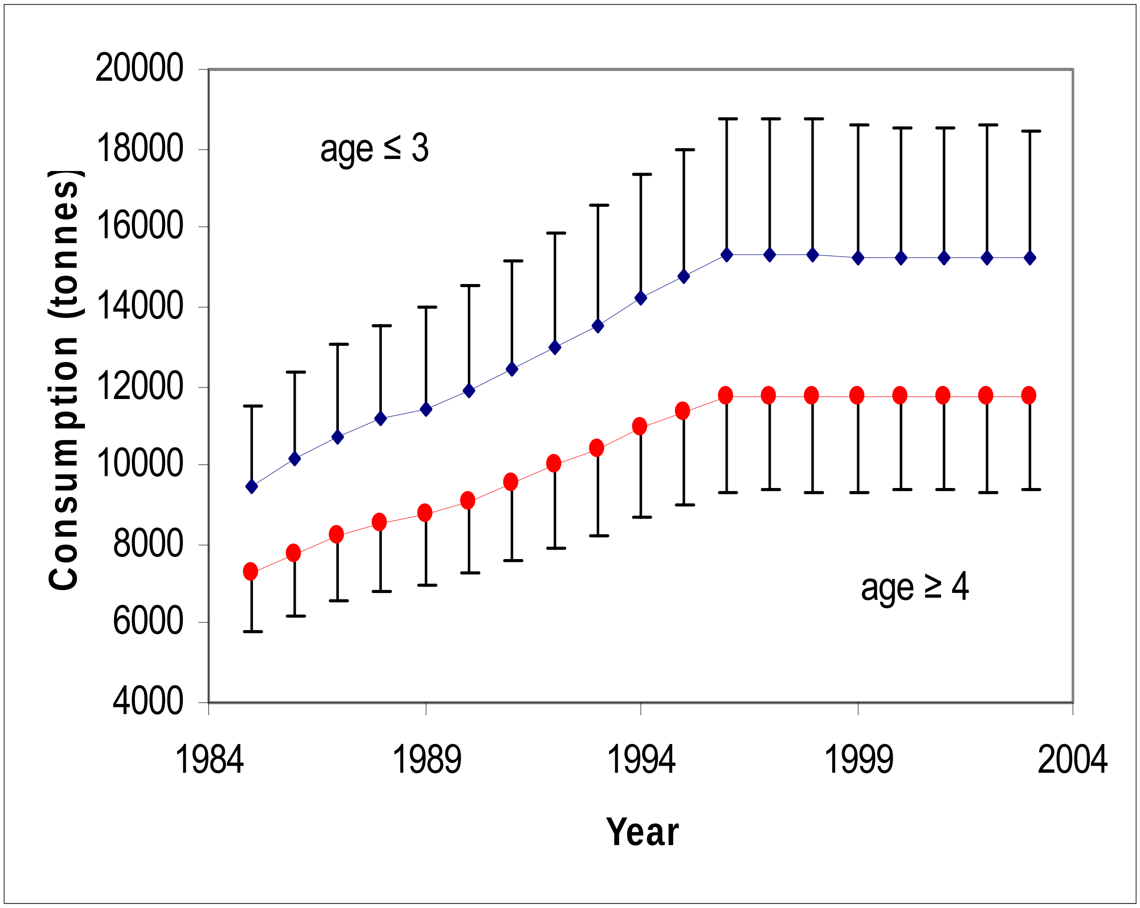


Figure 10. Estimated biomass (t) (+ or – 1 SD) of cod ≤3 years and cod greater ≥4 years, consumed by harp seals in 2001 in NAFO zone 4RS3Pn.