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Quantifying Some of the Major Sources of Uncertainty Associated with Estimates
of Harp Seal Prey Consumption. Part II: Uncertainty in Consumption Estimates
Associated with Population Size, Residency, Energy Requirement and Diet

by

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Abstract

Prey consumption by Northwest Atlantic harp seals, *Phoca groenlandica*, depends on population size, seasonal and spatial distribution, energy requirements, energy content of prey and diet composition. There is uncertainty in our knowledge of all these components. This carries through into uncertainty in any estimate of prey consumption. Our information ranges from sample estimates, sometimes with conventional measures of precision (standard errors), to guesses based on unquantified observation. We attempt to quantify the effect of some of the major sources of uncertainty, particularly with respect to the amount of Atlantic cod eaten in NAFO Div. 2J3KL (off southern Labrador and northeast Newfoundland). Our primary objective is to determine which components contribute most to the uncertainty, as a guide for research planning. However, a thorough quantification of uncertainty would also be useful in evaluating alternative management options for harp seals which have the objective of reducing possible impacts on prey. This work is divided into two parts. Part I looks in some detail at the accuracy of estimates of the size of the harp seal population through estimates of pup production and pregnancy rates. Part II examines the effect of this uncertainty on consumption as well as the effect of additional sources of uncertainty attributable to residency of harp seals, energy requirements, species composition of the diet in the inshore and offshore, and the calorific value of prey.

Introduction

The harp seal population in the Northwest Atlantic is estimated to number 4.8 million and to be increasing at about 5% per year (Shelton et al. 1995). There is considerable interest in what impact this might have on fish populations in the region, particularly northern cod which is presently under a fishing moratorium because of low abundance. The estimated harp seal population size trajectory for the period 1981 to 1994 from Shelton et al. (1995) was used in Stenson et al. (1995a) to calculate the consumption of Atlantic cod, capelin and Arctic cod. Fixed inputs were used for residency time, energy requirements and diet. From this analysis it was concluded that the harp seal population is consuming 2.8 million tons of marine organisms from the Newfoundland region (NAFO Divs. 2J3KL) of which 1.7 million tons is Arctic cod, 0.6 million tons capelin and 0.09 million tons Atlantic cod. A preliminary sensitivity analysis was carried out in Stenson et al. (1995a) by examining the effect of alternative plausible values for four key inputs. Changes in consumption values of up to 25% were obtained. Thus it was acknowledged that estimates of consumption are quite sensitive to changes in these inputs.

The purpose of the present work is to quantify the major sources of uncertainty in the calculation of consumption, primarily as a guide to where future research effort should be concentrated. However, a thorough quantification of uncertainty would also be useful in evaluating alternative management procedures for harp seals which have the objective of reducing possible impacts on prey. The robustness of alternative procedures to uncertainty, evaluated through simulation studies, should play a major role in selecting the best procedure. Although this study does not achieve the second objective, it attempts to lay the basis for further work in this direction.

A preliminary quantification of the uncertainty associated with the estimation of harp seal population size was carried out in Shelton et al. (1995). This is examined in much more detail in Part I by Warren et al. (this symposium). In Part II we look at the contribution to the uncertainty in the calculation of consumption contributed by the uncertainty in (i) population size, (ii) residency time in the study area, (iii) energy requirements, and (iv) diet, including species composition, energy content and assimilation efficiency. Conclusions are then drawn regarding where future research efforts should be concentrated in order to reduce uncertainty in the estimation of consumption. Consideration is also given to what further work needs to be carried out to arrive at reliable probability distributions of consumption by harp seals for use in decision making.

Sources of uncertainty

The uncertainty in the inputs is examined by Monte Carlo simulation. A single realization of consumption is generated by randomly selecting values for the inputs from distributions considered to describe the uncertainty in these inputs. This is repeated to give a set of realizations of consumption from which the effect of the factors being considered can be gauged. The analysis is conducted systematically, looking at each of the four main sources of uncertainty (population size, residency, energy requirement and diet) in turn, while holding all other inputs fixed at the values used in Stenson et al. (1995a). Consumption is calculated for the period 1981 to 1994 (the period for which diet data are available) and 50 randomly selected trajectories of consumption of cod are plotted. Frequency distributions for 500 realizations of the 1994 consumption of cod, capelin and Arctic cod are plotted and basic univariate statistics tabled. Following the analysis of the contribution to the uncertainty by the four different sources individually, all modelled sources of uncertainty are included and 1000 realizations are generated to get an impression of the possible overall uncertainty in the calculation of cod consumption. In order to examine the improvements that could be obtained with less certain inputs, each of the four sources of uncertainty are in turn treated as known exactly while the remaining three sources are treated as uncertain and 500 realizations are generated. A more detailed analysis of uncertainty is possible by examining the individual contributors to uncertainty within each of the four sources and this could be considered in the future.

Population size

In Shelton et al. (1995) the uncertainty in the harp seal population trajectory was examined by randomly sampling pairs of parameters (survival rate and selectivity) from a bivariate normal distribution defined by the parameter estimates, their standard errors and the correlation between the estimates. It was acknowledged that this provided only a partial exploration of the uncertainty because it was assumed that pregnancy rates and catches were known exactly. It was therefore considered an underestimate of the uncertainty. Also, the viability of the asymptotic standard errors from only six years of survey data is questionable.

In Part I of the present study Warren et al. (this volume) examines the uncertainty in the estimation of population size in much more detail. The uncertainty in both the estimates of pup production and the estimates of pregnancy rates are considered using an alternative non-asymptotic approach. It was found that the uncertainty in pregnancy rates had little additional effect when the uncertainty in population size is first accounted for. Results from the simulations to look at the uncertainty in pup production and the simulations in which both pup production and pregnancy rates are varied were combined to give 200 realizations of the population model parameter values. From these realizations Warren et al. (this symposium) developed a formulation from which pairs of parameter values can be randomly generated. First a realization of natural mortality, m , is generated from a normal distribution with mean and standard deviation estimated from the 200 realizations:

$$m \sim N[0.106880, 0.007228].$$

Then a value of s is generated from a normal distribution with a mean $\phi = 3.1219 - 30.3040m + 264.3880m^2$:

$$s \sim N[\phi, 0.004073].$$

As discussed in Warren et al. (this symposium) the problem with the non-asymptotic approach in which both the uncertainty in pregnancy rates and pup production are examined, is that the realizations of pregnancy rate need to be carried forward to the calculation of population size from the realization of the parameters of s and m obtained using those pregnancy rates. This is not possible in the parametric approach adopted here. It would require a full numerical simulation in which in each run a realization of pregnancy rate and a realization of pup production are generated from their respective probability distributions, the model is fitted and the realizations of the estimated parameters s and m used with the identical realization of pregnancy rate to generate a population trajectory. This approach was considered impractical in the time available. Since Warren et al. (this symposium) found that uncertainty in pregnancy rates inflates the overall uncertainty in population size marginally, the parametric approach is applied here with constant pregnancy rates with the knowledge that the uncertainty in population size is underestimated by some amount.

Residency time

Harp seals summer in Arctic waters and winter off Newfoundland and Labrador and in the Gulf of St Lawrence (Sergeant 1965, 1991). The general migration pattern has been determined from surveys, catches, aerial observations and anecdotal sightings, however detailed knowledge is limited (Stenson et al. 1995a). Uncertainty in the residency time was examined in a preliminary manner in Stenson et al. (1995a) by calculating consumption based on a fixed residency of 212 days (south of the northern boundary of Div. 2J) and then comparing this with a one month increase in residency. The increase in residency increased consumption by 12%. In this analysis we look in more detail at the uncertainty in the various factors that must be taken into account in determining the residency within Divs. 2J3KL and how this effects the calculation of consumption of Atlantic cod, capelin and Arctic cod.

Harp seals migrate south from the summer feeding grounds in the Arctic during the late fall. Based on catches and sightings summarized by Sergeant (1965, 1991), Stenson et al. (1995a) assumed that the average date of seals entered the study area (south of the Div. 2J/2H boundary) was November 15 and that they left on June 15. However, the migration may be spread over a relatively long period (Sergeant 1965) and the timing of the peak migration may vary greatly (Fisher 1955, Stenson unpublished data) with reports of seals within the study area from early October through July. Therefore, to quantify the uncertainty associated with this parameter, it was assumed that seals may enter the study area between October 15 and Dec 1 and leave between June 1 and July 15. This gives a range of possible residency time within the study area of between 182 and 272 days, as compared to the fixed value of 212 days used in Stenson et al. (1995a). A uniform distribution within this range was assumed. Once in the study area, a proportion of the population enters the Gulf of St. Lawrence after migrating through Divisions 2J3KL.

Stenson et al. (1995a) assumed a period of half a month for each of the southern and northward migrations (total 29 days), based upon the respective timing of fisheries along the mid-Labrador and northern Quebec coasts (Sergeant 1991). However, movements of individual seals obtained using satellite telemetry indicate that harp seals may move quickly between areas and then remain in one location for a considerable time. Therefore, the timing of the migration through the Newfoundland area may vary greatly. To quantify the uncertainty associated with this assumption, the amount of time animals destined for the Gulf spend within the study area was assumed to be described by a uniform distribution of between 15 and 45 days. Stenson et al. (1995a) assumed that the proportion of the population entering the Gulf was 0.25. This was based upon the assumption that approximately 1/3 of adults enter the Gulf to whelp but that some immatures remain off Newfoundland (Sergeant 1991). However, the proportion of total pup production which occurs in the Gulf can vary greatly among years. Comparing estimates obtained from comparable aerial surveys of both areas indicates that the proportion of total pup production which occurred in the Gulf rose from approximately 0.19 in 1990 (Stenson et al. 1993) to 0.34 in 1994 (Stenson et al. 1995b). Similarly, Winters (1978) estimated that the proportion of the total annual pup production which occurred in the Gulf from 1965 - 1977 varied between 0.51 and 0.13. Therefore, we assumed a uniform distribution within the range of 0.2 to 0.4. A proportion of the population remains in the Arctic throughout the year. A range of 0.15 to 0.25 was assumed compared with a fixed value of 0.2 used in Stenson et al. (1995a)

Energy requirement

In Stenson et al. (1995a) individual energy requirements were calculated using an allometric relationship linked to mass-at-age based on Kleiber (1975). Corrections for the additional energy requirements associated with growth, activity and assimilation efficiency are incorporated. The energy requirements for individual harp seals is assumed to be constant throughout the year. The equation is

$$GEI_i = GP_i * (AF * 70 * BM_i^{0.75}) / (ME)$$

where:

GEI = daily gross energy intake,

i = age group,

GP = growth premium,

AF = "activity factor",

BM = mean body mass for age group (kg),

ME = proportion of energy available to the animal (assimilation efficiency).

Body mass (BM) for each age group was based on measurements obtained from seals collected during April (Chabot et al., 1995). To account for uncertainty in body size we randomly resample body mass at age values from a normal distribution defined by the mean and standard deviation of these sample data: age 0 - N[25.449, 5.442]; age 1 - N[45.846, 7.279]; age 2 - N[56.041, 10.064]; age 3 - N[64.755, 10.354]; age 4 - N[74.863, 13.988]; age 5 - N[82.278, 13.648]; age 6 - N[85.384, 12.703]; age 7 - N[92.783, 12.563]; age 8 - N[93.487, 13.971]; age 9 - N[96.504, 13.958]; age 10 - N[101.763, 13.128]; age 11 - N[101.763, 13.128]; age 12+ - N[101.763, 13.128].

Lavigne et al. (1986) reviewed the metabolic literature of seals and suggested that growing phocids had basal metabolic rates twice that of older animals. The increased energy required for growth was applied to the metabolic calculations for younger seals in decreasing increments from GP=2.25 for one-yr olds to 1.25 for 5 yr olds. These values were used in Stenson et al. (1995a). Alternative values are given in Olesiuk (1993). In this analysis, each realization randomly selects between the Lavigne and Olesiuk values with equal probability. Further information on this input may allow a more comprehensive examination of the uncertainty contributed by this source in the future.

Studies of the energy requirement of captive and wild seals indicate that estimates of the average daily energy requirement vary between 1.7 and 3 times the basal metabolic rate estimated using body mass (Castellini et al., 1992; Innes et al., 1987; Worthy, 1987a; Worthy, 1987b; Worthy, 1990). Since most published values cluster near a value of 2, an activity factor (AF) of 2 was chosen in Stenson et al. (1995a) to approximate the energy requirements of activity of free-ranging harp seals. To account for the uncertainty, activity factors are randomly sampled from a triangular distribution. The distribution extends from 1.7 to 3 and has a peak at 2. The area of the triangle is made to sum to 1 by setting the height to 1.5385. A rejection method was used to randomly sample from this distribution. Two random variates, $X \sim U[1.7, 3]$ and $Y \sim [0, 1.5385]$ are generated in each realization until the coordinates are within the area of the triangle. The X value for realizations within the triangle is taken to be a realization of the activity factor.

Diet

Considerable seasonal, geographic, and annual variability exists in the diet of harp seals (Lawson et al. in press; Stenson et al. 1995a; Lawson and Stenson in press). Stenson et al. (1995) presented information on the diet of harp seals in Newfoundland separated into winter and summer periods for offshore diets (1991- 1994 combined) and 6 years for which reconstructed stomach contents of nearshore harp seals were available (1982, 1986, 1990-1993). To express the uncertainty in the proportion of prey in the diet, they estimated consumption by harp seals in Newfoundland based on the annual diets as well as consumption estimated using the average of the 14 annual diet averages. The uncertainty associated with using the overall average diet was illustrated by calculating the 95% confidence intervals around the estimates of consumption by randomly resampling the 14 diets with replacement 1,000 times.

In the present analysis the stomach sample data were pooled into four sets, inshore-winter (n=674), inshore-summer (n=495), offshore-winter (n=83) and offshore-summer (n=144). Only data from 1990 onwards were included. Samples within each of these four sets are relatively homogeneous (Warren pers. com.). The contribution of each diet to the overall estimate of annual consumption was weighted according to Stenson et al. (1995a). These weightings represent the relative amount of energy obtained from each of the four sets. The relative weightings used for winter:summer are 0.6241:0.3759 and for inshore:offshore are 0.45:0.55.

The proportion of energy contained in the food which is available to the harp seals (ME, assimilation efficiency) has not been measured directly for most of the major prey items. Published values range from 72.2% for shrimp (Keiver et al., 1984) to 94% for capelin (Mårtensson et al., 1994). Following Stenson et al. (1995a) the mean assimilation efficiency are calculated for each of the four realized sets of diet data using fixed prey-specific values. Energy density of prey were based on the average of published values for the major species, where available (e.g. Anonymous 1969, Croxall and Prince 1982, Hislop et al. 1991, Holdway and Beamish 1984, Hop 1994, Hopkins et al. 1989, Krzynowek and Murphy 1987, Nettleship 1992, Nordøy and Blix 1988, Steimle Jr., Terranova 1985) and analyses performed at DFO (Lawson unpublished data). Following Stenson et al. (1995a) the mean energy content of the prey is calculated based on the diet composition.

It should be noted that this treatment of the diet data in the present analysis is different than that of Stenson et al. (1995a). In particular, the 1982 and 1986 diet data, which are significantly different from the more recent diet data (Warren, unpublished analysis) are not used. Further, the diet data from 1990 onwards, within each of the four sets, are treated as if they are all equally likely realizations of the 1994 diet (i.e. there have been no systematic changes over the period). In the calculation of a cod consumption trajectory, the assumption is made that the realization of diet applies over the period 1981 to 1994, which does not necessarily hold.

Results and Discussion

The 50 realizations of cod consumption over the period 1981 to 1994 shows the overall increase caused by the increase in the seal population (Fig 1). The relative contribution to the uncertainty from the four sources as illustrated in these plots shows that uncertainty in population size has the least effect and uncertainty in diet the greatest effect. The contribution by uncertainty in residency and energy requirements are similar. Note that the uncertainty in diet examined here follows the approach described above (resampling from four relative homogeneous sets of the data for the post 1990 period whereas the diet is fixed at the values given in Stenson et al. (1995a) in the other three analyses.

The uncertainty in consumption of cod, capelin and Arctic cod contributed by each of the four sources of uncertainty alone are illustrated in the frequency distributions for 500 realizations of consumption (Figs. 2 - 4). Descriptive statistics for the distribution of cod consumption are given in Table 1. With respect to cod consumption (Fig. 2, Table 1), uncertainty in diet made the greatest contribution to uncertainty in cod consumption (CV=28%) and uncertainty in population size made the smallest contribution (CV=4%). Uncertainty in energy requirement and residency made equal contributions (CV=12%). It is of interest that the fifth percentile for analysis in which uncertainty in diet is accounted for is not any lower than in the other analyses, however the ninetieth percentile is much higher, giving a large 90% probability range. Recall that the distribution in which diet is varied does not centre around the 88,000 tons value given in Stenson et al. (1995a) because of the different treatment of the diet data.

With respect to capelin consumption (Fig. 3), uncertainty in population has a relatively small effect compared to uncertainty in the other sources. The spread in the distribution caused by uncertainty in residency and energy requirements are similar, whereas the spread resulting from uncertainty in diet is only slightly larger.

Uncertainty in Arctic cod consumption (Fig. 4) is relatively small when uncertainty in harp seal population size is taken into account. Uncertainty in both residency and energy requirements make relatively large contributions whereas the contribution to uncertainty by diet is approximately the same as that of population size.

When all four sources of uncertainty are introduced simultaneously, there is a wide range in the amount of cod, capelin and Arctic cod consumed, as might be expected (Fig. 5, Table 1). In the 50 realizations of cod consumption over the period 1981 to 1994, cod consumption ranged from about 30,000 tons to 150,000 tons in 1980 and about 50,000 tons to 300,000 tons in 1994. The distributions from the 1000 realizations of consumption for cod, capelin and Arctic cod are all slightly skewed to the right, i.e. there is a small probability of consumption being quite a bit higher than the mean, but less probability that consumption is much smaller than the mean. The CV in cod consumption is 35% with fifth and ninetieth percentiles of 73,000 tons and 232,000 tons respectively. Uncertainty in capelin consumption ranges from 360,000 tons to 1,500,000 tons and Arctic cod consumption from 560,000 tons to 1,700,000 tons.

The reduction in overall uncertainty in cod consumption obtained by, in turn, treating each of the four individual sources of uncertainty as known exactly is summarized in Table 1. As anticipated, knowing harp seal population size exactly gives the smallest improvement in the CV - from 35.1% to 34.7%. Improvements obtained by knowing either the residency time of harp seals in the study area or their energy requirements exactly are similar (CV reduced to 31.7% and 30.2% respectively). Exact information on diet reduces the CV on the uncertainty to 18.3%. A similar CV would pertain if the diet as used in Stenson et al. (1995a) were used. Note that there is little improvement in the minimum estimate by removing uncertainty in any of the sources other than diet.

These results suggest that the largest improvements in the precision of estimates of harp seal consumption of cod will be obtained by improved knowledge of diet composition. This conclusion is based on the assumption that within each of the four relatively homogeneous diet sets for the period 1990 onwards, the samples vary according to random sampling error only and there is not systematic variability that can be accounted for (e.g. a time trend in diet in the period 1990 onwards).

The conclusion made in the case of cod consumption with respect to knowing diet exactly does not appear to pertain to capelin and Arctic cod consumption. For capelin, uncertainty in residency, energy requirements and diet contribute approximately equally, whereas in the case of Arctic cod, uncertainty in residency and energy requirement contribute the most.

While better information for all four groups of inputs into the estimation of harp seal consumption would be very valuable, the present study suggests that improvements in the diet data will yield the most benefit with respect to the improvements in the estimate of cod consumed by harp seals. Further work could be carried out at a finer scale by

examining the contribution of uncertainty by the various factors within each of the four sources. The present analysis only looks at the improvement obtained by going from a situation in which the input is uncertain to one in which it is known exactly. More detailed analysis could look at the effect of certain percentage reductions in the uncertainty of selected inputs and the dollar cost of making such reductions. This would allow research planning of a more detailed kind than simply the suggestion that "we need better diet data".

It is of interest that the uncertainty in population size is the smallest contributor to uncertainty in consumption. It is also one of the few inputs for which a formal estimate of the uncertainty is available. Although intensification of the pup survey program through more frequent surveys may not lead to a large improvement in the uncertainty regarding harp seal consumption of prey species, the more time-consuming simulation approach described above should be explored to examine the potential improvement that may result from better pregnancy data. Although Part I of this study (Warren et al., this symposium) suggests that the contribution by uncertainty in pregnancy rate is small, there are considerable difficulties in interpreting the current data set (Sjare, this symposium).

Considerably more work remains to be done before a thorough quantification of the uncertainty regarding cod consumption can be arrived at for use in decision making. Nevertheless, in the interim, decision makers should be cognizant of the fact the CV in the current estimate of cod consumption is of the order of 35%. Over-reliance on a point estimate should be avoided where possible.

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Source	Mean	Median	Std Dev	CV	Min	Max	P5	P95	90% P range
Source added									
Population size	90137.42	90877.28	3662.75	4.06352	72440.62	121312.9	84032.11	93329.41	9297.30
Residency time	89348.25	89857.01	10544.04	11.8011	66250.81	116787.71	72801.78	106830.05	34028.27
Energy requirement	88169.91	86916.14	10533.78	11.9471	62452.92	118916.16	72976.57	106943.35	33966.78
Diet composition - A	128665.79	125876.11	35559.71	27.6373	49080.18	271084.94	72658.90	194145.19	121486.29
All sources together									
Population size	140807.54	135128.17	49554.66	35.1313	49554.66	416255.59	72544.34	232100.10	159555.76
Source removed									
Population size	132334.32	125723.74	45965.76	34.7346	42643.16	284215.86	70475.86	225670.79	155194.93
Residency time	138386.73	134900.79	43994.29	31.7908	47679.57	303639.29	78898.51	216429.85	137531.34
Energy requirement	143947.34	140508.56	43419.02	30.1631	46892.69	330059.46	80260.37	219815.15	139554.78
Diet composition - A	130693.61	128340.73	23955.95	18.3299	79386.40	237204.78	95898.80	172837.94	76739.14
Diet composition - B	91818.32	90499.57	16144.72	17.5833	56766.03	149070.29	67878.98	120207.11	52328.13

Table 1. Descriptive statistics for the distributions of 500 realizations of cod consumption including each source of uncertainty separately, all sources together and then removing each source in turn. Note that "Diet - A" refers to the diet grouped into four sets representative of inshore, offshore, summer and winter and that "Diet - B" is the diet as used in Stenson et al. (1995b). The analysis introducing each source of uncertainty separately uses "Diet - B" except for when diet itself is varied when "Diet - A" is used.

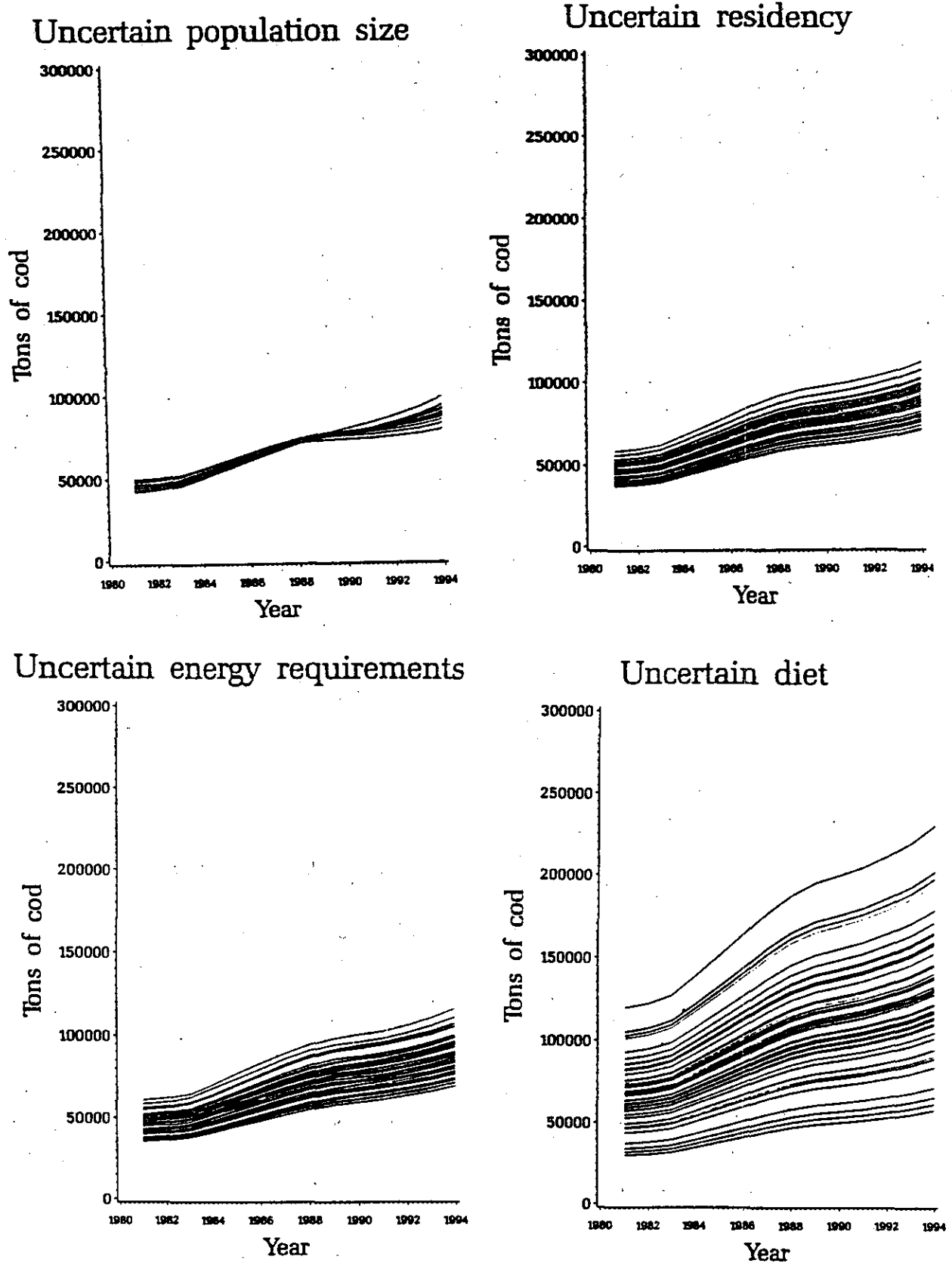


Fig. 1. Plots of 50 realizations of cod consumption trajectories for the period 1981 to 1994 taking into account uncertainty in population size, residency, energy requirements and diet.

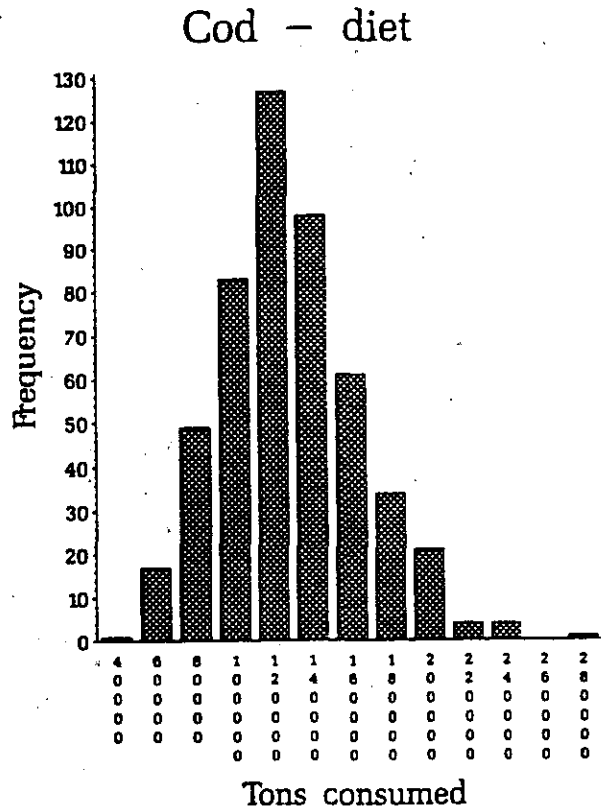
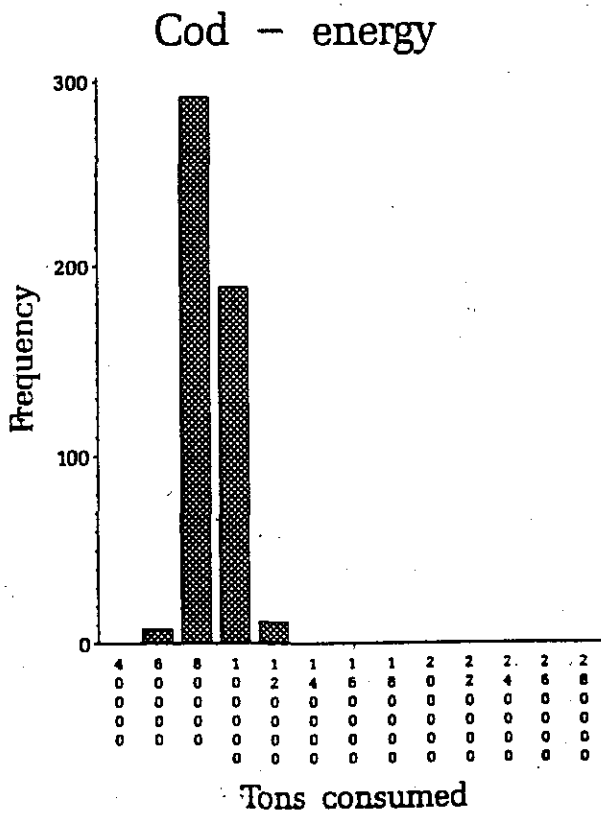
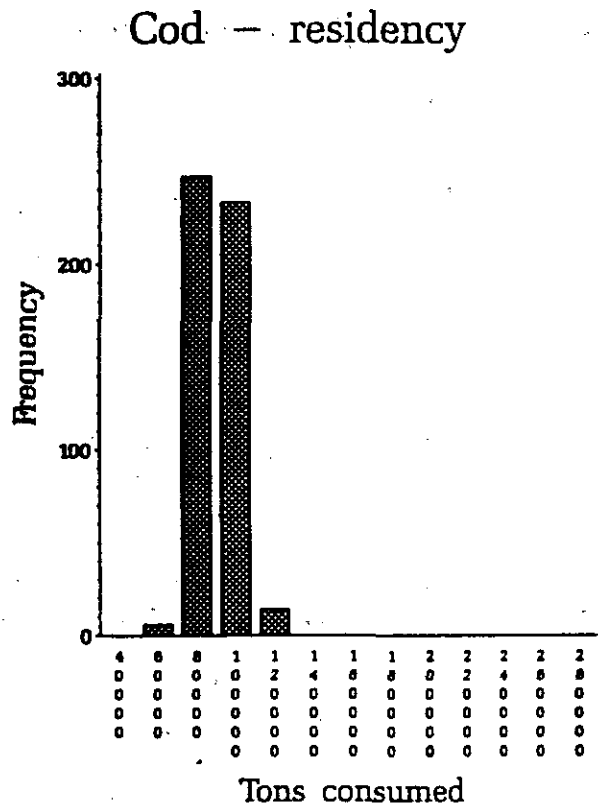
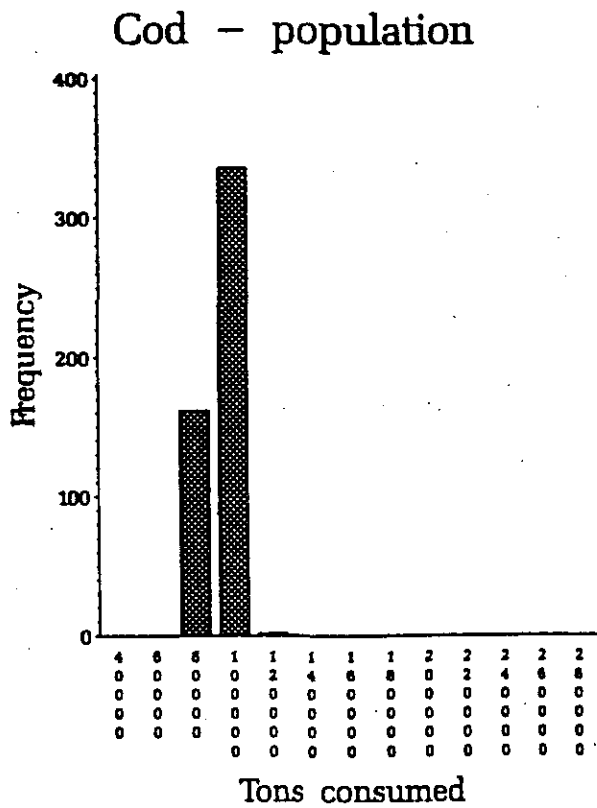


Fig. 2. Frequency distributions of 500 realizations of cod consumption taking into account uncertainty in population size, residency, energy requirements and diet.

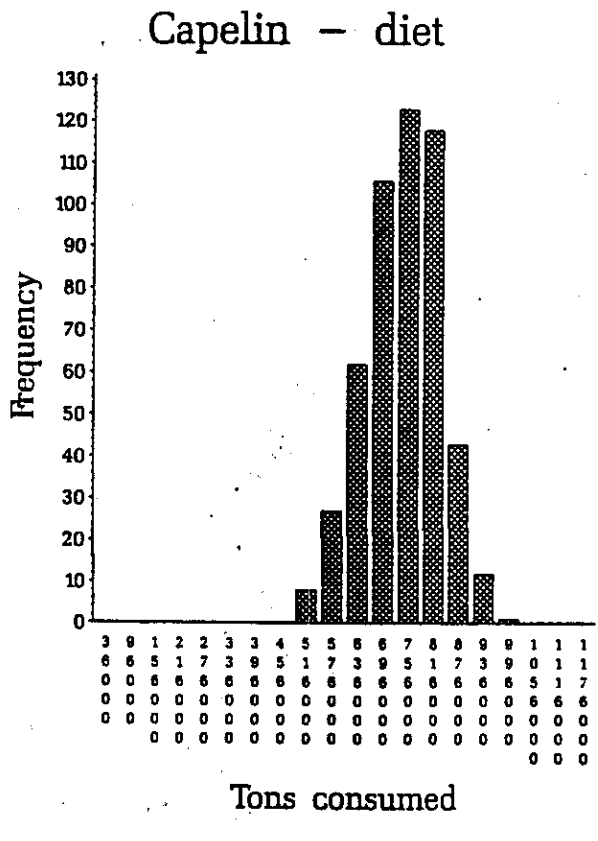
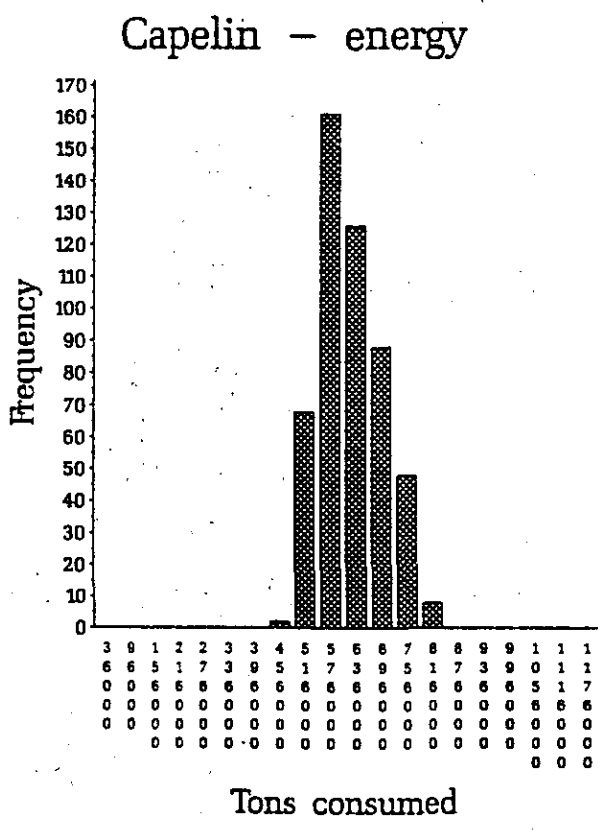
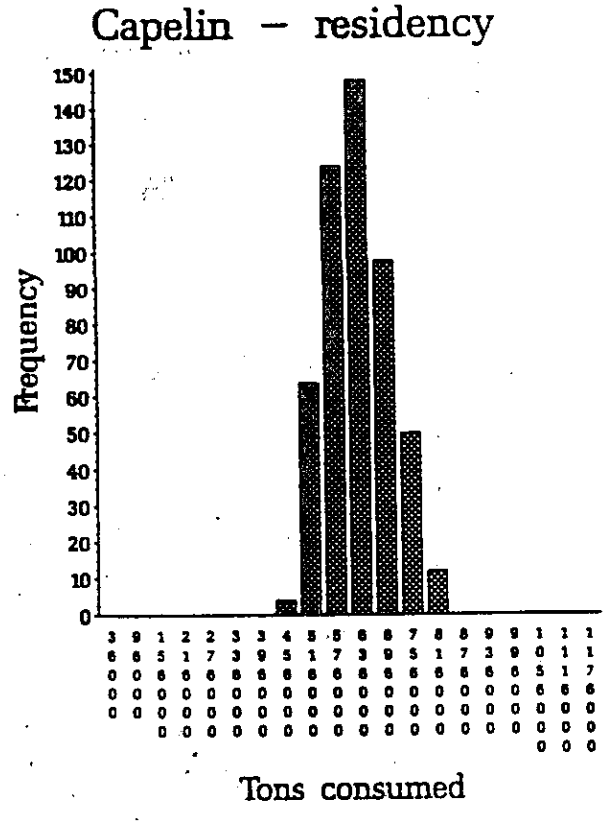
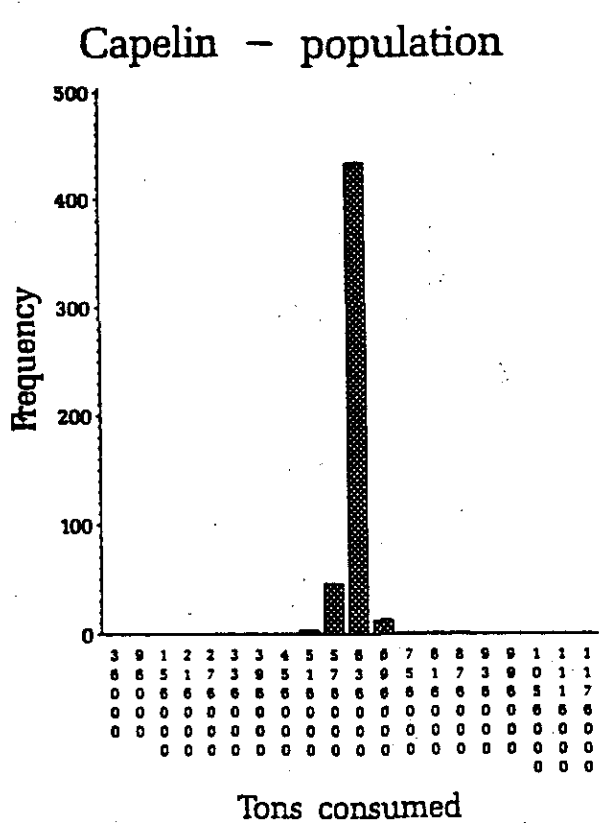


Fig. 3. Frequency distributions of 500 realizations of capelin consumption taking into account uncertainty in population size, residency, energy requirements and diet.

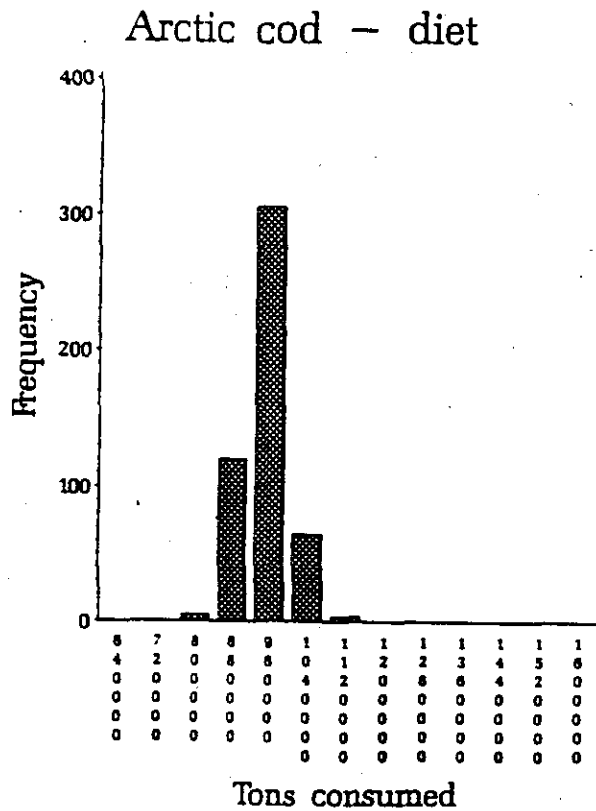
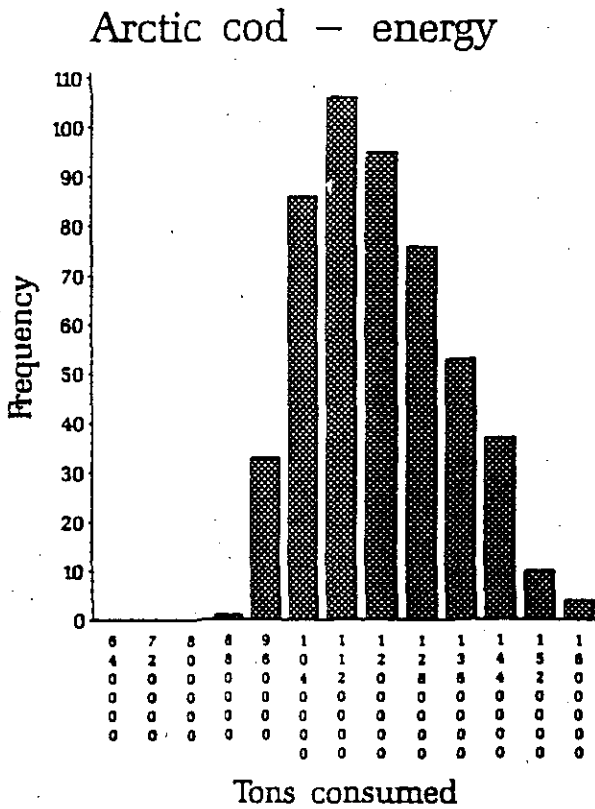
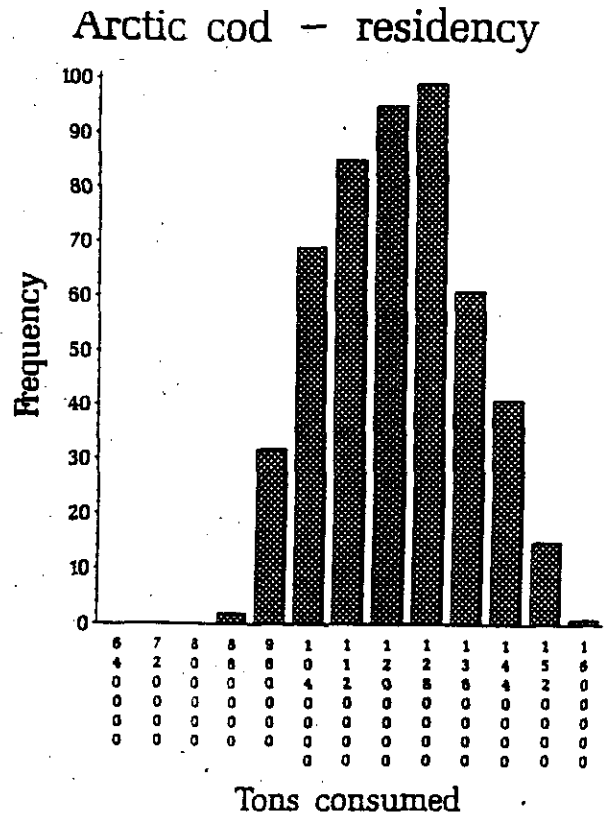
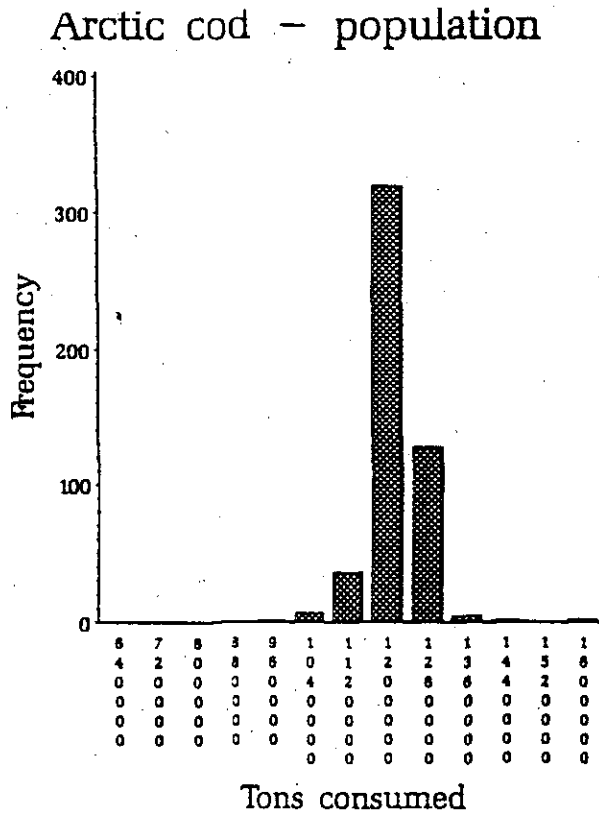


Fig. 4. Frequency distributions of 500 realizations of Arctic cod consumption taking into account uncertainty in population size, residency, energy requirements and diet.

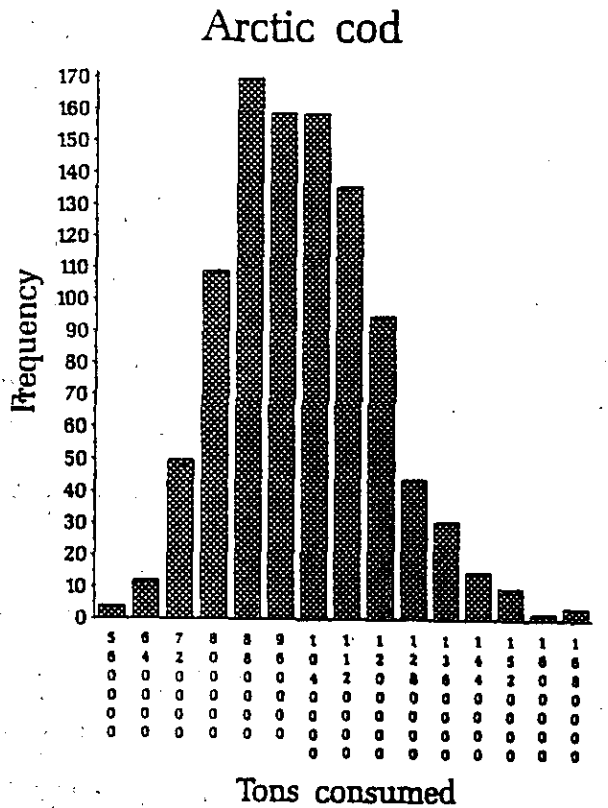
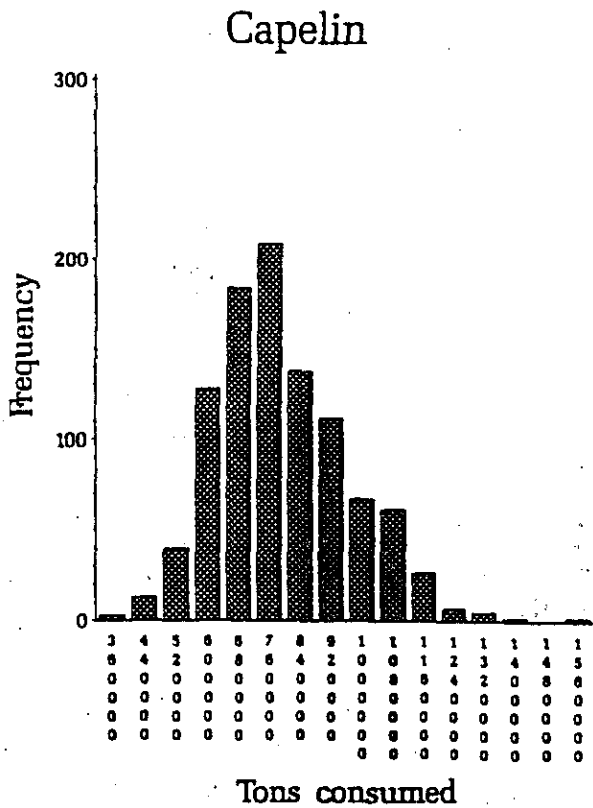
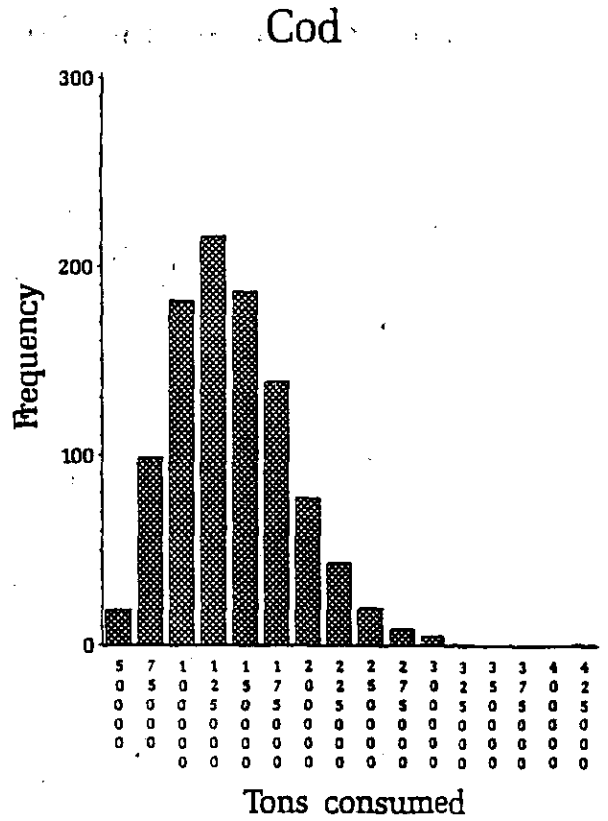
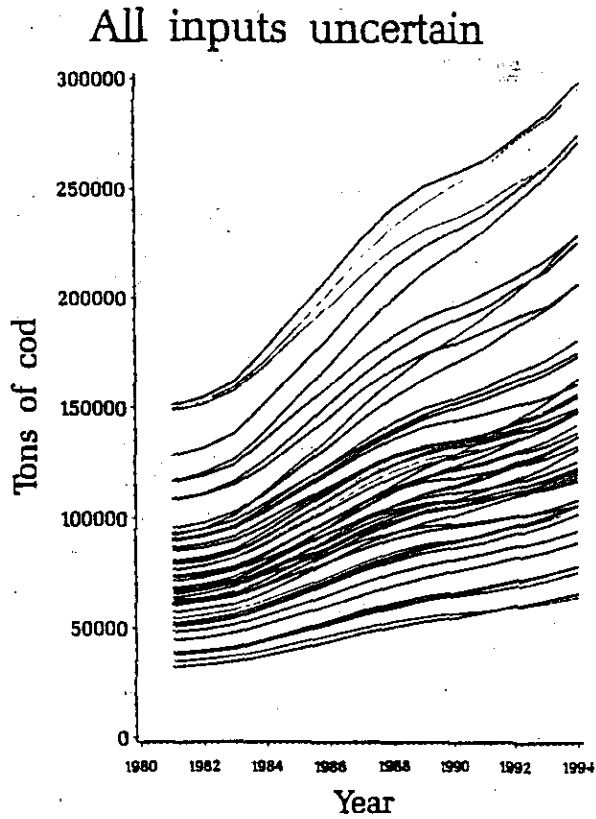


Fig. 5. Plot of 50 realizations of cod consumption trajectories over the period 1981 to 1994 together with frequency distributions of cod, capelin and Arctic cod consumption from 1000 realizations taking into account all four sources of uncertainty simultaneously.