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Predation of Atlantic Cod, Capelin, and Arctic Cod by Harp Seals in Atlantic Canada

by

G. B. Stenson[1], M. O. Hammill[2], J. W. Lawson[3]

[1]Department of Fisheries and Oceans, Science Branch
P. O. Box 5667, St. John's, Newfoundland, Canada A1C 5X1

[2]Department of Fisheries and Oceans, Science Branch
P. O. Box 1000, Mont Joli, Quebec, Canada G5H 3Z4

[3]Ocean Sciences Centre, Memorial University of Newfoundland
St. John's, Newfoundland, Canada A1C 5S7

Abstract

Current estimates of harp seal abundance indicate that the total population size in eastern Canada in 1994 was approximately 4.8 million (95% C.I. 4.1 - 5.0 million) animals. To estimate the consumption of major fish prey by harp seals off the coast of Newfoundland and in the Gulf of St. Lawrence, a model incorporating age-specific estimates of energy requirements, population size, seasonal distribution and diets was constructed. Total prey consumption increased from 3.6 million to 6.9 million tonnes between 1981 and 1994. The proportions of prey obtained in the Arctic and Newfoundland areas were similar (46% and 40% respectively), while 14% was consumed in the Gulf. The major prey off Newfoundland was Arctic cod and capelin. Based on an average diet, harp seals consumed an estimated 1.2 million tonnes (95% C.I. 735,000 - 1.7 million) of Arctic cod, and 620,000 tonnes (95% C.I. 288,000 - 1.0 million) of capelin in 1994. An estimated 88,000 tonnes (95% C.I. 46,000 - 140,000) of Atlantic cod were also consumed. In the Gulf, harp seals consumed an estimated 445,000 tonnes (95% C.I. 208,000 - 727,000) of capelin, 20,000 tonnes (95% C.I. 0 - 48,000) of Arctic cod, and estimated 54,000 tonnes (95% C.I. 14,000 - 102,000) of Atlantic cod in 1994. Incorporating seasonal, geographic and annual variation in the diet provide additional information on trends in consumption. The basic assumptions of the model were varied to assess its sensitivity. Changes in the energetic costs of activity and growth, abundance, residency period, or the proportion of energy obtained from offshore areas can affect estimates of total consumption significantly.

Introduction

Harp seals are a migratory species found throughout the northwest Atlantic where they feed upon a variety of fish and invertebrate species (Sergeant 1973, 1991; Beck et al. 1993; Lawson and Stenson 1995; Lawson et al. 1994). Recent studies indicate that their numbers have been increasing since the early 1970s and may now be in the order of 4.8 million (Shelton et al. 1995). The impact of this abundant predator on the declining commercial fish stocks off the Atlantic coast of Canada is unknown. However, before the possible impact can be assessed, the total amount of each prey species consumed must be estimated.

The consumption of fish by marine mammal predators has been estimated by a number of authors using bioenergetic models (Hammill and Mohn, 1994; Markussen and Øritsland, 1991; Mohn and Bowen, 1994; Øritsland and Markussen, 1990; Ryg and Øritsland, 1991, Olesiuk, 1993). The energy requirements of individual seals were estimated and then extrapolated to the entire population. The proportion of energy obtained from various prey species and the amount consumed was estimated using information on the seasonal distribution of seals, the composition of their diet in various areas, and the energy content of the prey.

The objective of this study is to estimate consumption of Arctic cod (*Boreogadus saida*), capelin (*Mallotus villosus*) and Atlantic cod (*Gadus morhua*) by harp seals in the waters of Gulf of St. Lawrence and off Newfoundland. To determine the sensitivity of the consumption estimates to the basic parameters used in the model, total consumption was examined using different assumptions of population size, energy requirements for activity and growth, seasonal distribution, and seasonal and geographic variation in the diet.

Model Inputs

Abundance:

Shelton et al. (1995) present estimates of numbers at age for northwest Atlantic harp seals from 1955 - 1994. Under the assumption that mortality was constant for all age groups, the model indicated that the population declined from an estimated 2.8 million seals in 1955 to approximately 1.8 in the early 1970s (Figure 1). Since then it has increased, from approximately 2.5 million at the start of the study period to approximately 4.8 million (range 4.1 - 5.0) in 1994.

In a second run of the model, Shelton et al. (1995) assumed that pup mortality was greater than that of older seals. The resulting population is lower, reaching an estimated 4.5 million in 1994 (Figure 1). To determine the importance of population size, consumption in southern Atlantic waters (Gulf and Newfoundland) was also estimated using the lower population.

Energy Requirements:

Energy requirements were assumed to be constant throughout the year. Individual energy requirements were calculated using an allometric relationship linked to mass-at-age based on Kleiber (1975). A correction for the additional energy requirements associated with activity and growth was included:

$$\mathbf{GEI_i = GP_i \cdot (AF \cdot 70 \cdot BM_i^{0.75}) / (ME)}$$

Where:

GEI = daily gross energy intake
i = age group
GP = growth premium
AF = "activity factor" (multiplier of BMR)
BM = mean body mass for age group (kg)
ME = proportion of energy available to the animal.

Body mass (BM) was based on measurements obtained from seals collected during April (Table 1). The proportion of energy contained in the food which is available to the animal (ME) has been estimated by Ronald et al. (1984) to be 0.83 for grey seals and 0.827 for ringed seals (Ryg and Øritsland, 1991). A value of 0.83 was used for this model.

Studies of the energy requirement of captive and wild seals indicate that the estimates of the average daily energy requirements vary between 1.7 and 3 times the basal metabolic rate estimated from body mass (Worthy, 1990). An activity factor (AF) of 2 was chosen to approximate the energy requirements of activity of free-ranging seals. To investigate the importance of this assumption, total Atlantic (Newfoundland and Gulf) consumption was also estimated using an activity factor of 2.5.

The increased energy required for growth (GP) was applied to the metabolic calculations based on estimates obtained from Lavigne et al. (1986; Table 2). The influence of this assumption was examined by estimating Atlantic consumption using the slightly lower growth premium proposed by Olesiuk (1993) for harbour seals (Table 2).

Seasonal Distribution of Harp Seals:

Harp seals are a migratory species that summer in Arctic waters, primarily Canadian Arctic and West Greenland, and winter off the coast of Newfoundland and Labrador, or in the Gulf of St. Lawrence (Sergeant, 1965; Sergeant, 1991). The proportion of energy obtained from each of these areas was estimated using the proportion of time spent in each region.

Although the general migratory pattern has been determined from marine mammal surveys, catch records, aerial observations and anecdotal sightings (Sergeant 1965; Sergeant 1991; Stenson and Kavanagh 1993; Stenson unpublished data), detailed knowledge of the seasonal distribution of harp seals is very limited . Harp seals migrate from the summer feeding grounds in the Arctic in the late fall. When they reach the study areas, some seals remain off the coast of Newfoundland while other move into the Gulf of St. Lawrence. They form large whelping concentrations in late February/early March near the Iles de la Madeleine or off southern Labrador. Following breeding, seals disperse briefly. From mid April to mid May they congregate into large moulting concentrations after which they eventually migrate northward.

The timing of the migrations appears to be variable and may be influenced by prey availability, ice cover, or water temperature.

Harp seals are considered be primarily a nearshore species (Sergeant, 1991). However, this is based on traditional sources of information such as catch statistics and tag returns that are biased towards nearshore areas. Recent studies indicate that harp seals are also present in offshore waters although their numbers cannot be estimated (Stenson and Kavanagh 1993; Stenson, unpublished data).

The total annual energy required by adults (greater than 4 years of age) and pups or juveniles was divided into two seasons (October - March and April-September), roughly corresponding to the two periods of major migration. For each season, the proportion of the total energy requirements obtained from each of three areas (eastern Newfoundland, Gulf of St. Lawrence, and Arctic; Table 3) was estimated assuming that:

a) harp seals enter the study area (south of 56°N) November 15 and leave June 15 (212 days).

b) 20% of juveniles and pups remain in the Arctic throughout the year (Anonymous, 1986; Kapel, 1982; Larsen, 1985).

c) 25% of the population is present in the Gulf of St. Lawrence between December 1 and May 31.

d) 5% of the seals remain in the study area throughout the year; 25% of these seals stay in the Gulf while 75% stay off Newfoundland.

In recent years, seals have been reported to arrive along the coast of Newfoundland earlier in the fall and to remain longer before migrating northward. To estimate the importance of a longer residency time, we estimated total Atlantic consumption after increasing the residency period by one month (November 1-June 30).

Composition of Harp Seal Diets:

The species composition of the diet was determined by identifying hard parts in the stomachs. The proportions of each prey species consumed was estimated by reconstructing the wet weights of the prey ingested using either undigested remains or species specific weight/otoliths regressions (for examples see Murie and Lavigne 1991, Beck et al. 1993, Lawson et al. 1994).

The proportion of major prey in the average diet of harp seals feeding in the Gulf of St. Lawrence based upon reconstructed wet weights was obtained from five samples (Table 4). Two small samples were collected from the St. Lawrence Estuary in winter (January - February 1983; Murie and Lavigne 1991) and spring (April 1988 - 1990; Beck et al. 1993). A third, larger, sample was collected during the breeding period around the Magdalen Islands (Beck et al. 1993). The two remaining samples were from seals collected along the west and south coasts of Newfoundland (Lawson and Stenson 1995, unpublished data), primarily between 1986 and 1993.

The information available on the diet of harp seals feeding in the waters off southern Labrador and eastern Newfoundland is more extensive. A comprehensive collection program was carried out between 1981 and 1993 (Lawson and Stenson, 1995, unpublished data; Lawson et al., 1994). The majority of samples were taken in nearshore areas (< 30 km from the headlands of bays). Prior to 1985, most samples were collected from the northeast coast of Newfoundland; after 1984, sampling effort was reasonably consistent across eastern Newfoundland and southern Labrador. Samples were collected from all months, with the majority taken between November and June. In recent years (1992-1994) samples were obtained from offshore areas (> 100 km from shore), primarily along the northern edge of the Grand Banks during winter and on the bank during the spring. The proportion of stomachs containing a particular prey item (prevalence) was estimated for all years. For the years 1982, 1986, and 1990-1994, estimates of the proportion of prey in the diet was estimated by reconstructing the wet weights of prey ingested using hard parts, primarily otoliths. The proportion of each prey species in the diet based on reconstruction was also determined for seals collected in offshore areas.

The diet of harp seals varies seasonally, geographically and annually (Lawson and Stenson, 1995; Lawson et al., 1994). Therefore, the diet data from Newfoundland was divided into two seasons (winter: October-March and summer: April-September), and into nearshore and offshore components. Annual estimates of the diet were available during both seasons for the nearshore component. However, due to small samples sizes, the offshore component was pooled across years and a single diet for each season used for all years (Table 5). An average energy density of prey was calculated for each season and area.

For the initial run of the model, the 14 samples from Newfoundland (12 nearshore, 2 offshore) and the 5 samples from the Gulf were averaged and the mean proportions and energy density of prey applied to all years and seasons for each area (Table 6). The 95 % confidence limits were approximated by a bootstrapping procedure (Efron, 1982; Efron and Tibshirani, 1993). The possible diets were resampled with replacement 1,000 times.

The importance of annual, seasonal and geographic variations in the diet was determined by using the proportion of each species present in each of the 14 diet samples (Table 5) separately. Reconstructed wet weights of all prey species were available for the years 1982, 1986 and 1990-1993. The proportion of prey in the nearshore diet for years for which reconstructed wet weights were not available (1981, 1982-1985, 1987-1989) was estimated using prey-specific regressions of prevalence and weight calculated using data from the six years for which both were available (Table 7). Due to variance around the regression, the total weight estimates for Atlantic cod, capelin and Arctic cod were occasionally greater than 100%. To solve this problem, all weight percentages were corrected so that the total weight accounted for by these four species was equal to the mean values for the appropriate season (summer: mean=72.5%, SE =4.2 and winter: mean=84.17%, SE=2.04). The regression-derived estimates of wet weight of the four prey species are summarized in Table 8.

The proportion of the annual energy requirements obtained by harp seals in offshore areas is unknown. Therefore, it was assumed that the seals were randomly distributed off Newfoundland and that the amount of energy obtained from areas represented by the nearshore or offshore diets were proportional to their area. Based on the areas in which the samples were collected (<30 km) and the possible movements of food containing seals prior to being captured (~60-70 km in 2 hours), the nearshore diets were assumed to represent an area within 100 km of the shore. The offshore diet was assumed to represent the remaining area out to the 400 m depth contour which is the area in which harp seals have been observed (Stenson and Kavanagh 1993, Stenson and Sjare, unpublished data). Based on these assumptions, the nearshore diet represents 45% of the energy obtained from Newfoundland waters while offshore diets represent 55%.

Consumption Estimates

Total consumption of prey in each of the three areas (Arctic, Newfoundland and Gulf) was estimated using the parameters described above. The mean energy density of prey consumed in the Arctic was assumed to be the same as Newfoundland which consisted of a mixture of Arctic and Atlantic prey species.

To estimate the sensitivity of the model to basic parameters, individual parameters were varied as described above and consumption in Atlantic waters calculated. The parameters used in the initial and alternative runs are summarized in Table 9. The parameters described for the initial run were used to estimated consumption of individual prey species.

The consumption of individual prey species was estimated using the average proportion of each species in the diet. An estimate of the variance associated with the proportion of each species in the diet was obtained by bootstrapping, treating each period or location as a sample. Consumption in Newfoundland waters was also estimated incorporating annual, seasonal and geographic variation in the diet.

Results

Total Consumption

The total consumption for the harp seal population was estimated to have increased from 3.6 million tonnes of prey in 1981 to 6.9 million in 1994 (Figure 2). Similar proportions of prey were obtained in the Arctic and Newfoundland areas (46% and 40%, respectively) while the Gulf accounted for 14% of the total. The amount of prey consumed in southern Atlantic areas almost doubled, rising from 1.45 to 2.79 million tonnes in Newfoundland and 498,000 to 960,000 tonnes in the Gulf.

These estimates of consumption are sensitive to changes in the model assumptions. Of those examined, the most critical is the 'activity factor' used to account for the energetic costs of swimming and other normal activities. Increasing AF from 2 to 2.5 resulted in a 25% increase in the energy required and therefore, prey consumed (Figure 3, Table 9). The amount of prey consumed was reduced by changing the population estimate and assumed cost of growth for young seals ('growth premium'). Using the numbers at age derived from the population model with increased pup mortality and a lower overall population of 4.5 million (Shelton et al., 1995) decreased the estimate of consumption in southern Atlantic waters during 1994 by 12% from 3.7 million tonnes to 3.3 million (Figure 3, Table 9). Replacing the estimates of energy required for growth obtained from Lavigne et al. (1986) with the lower estimates of Olesiuk (1993) also resulted in a slight reduction of 7% in the consumption (Figure 3, Table 9).

Increasing the time during which seals are present in southern waters slightly (one month or 14%) did not affect the overall consumption but did increase the estimate of consumption in the Gulf and Newfoundland by 12% (Figure 3, Table 9).

Atlantic Cod Consumption

Atlantic cod consumption in the Gulf of St. Lawrence was estimated to have increased from 28,000 tonnes in 1981 to 54,000 tonnes in 1994 (Figure 4). Because of the large variability in the diet samples, the 95% confidence limits were wide, ranging from 14,000 to 102,000 in 1994.

Using the average proportion of Atlantic cod in the diet, consumption off Newfoundland increased from 46,000 to 88,000 tonnes between 1981 and 1994 (Figure 5). As in the Gulf, the variability in these estimates, indicated by the 95% confidence limits, was close to 50%, ranging from 46,000 to 140,000 in 1994. A slightly different pattern of Atlantic cod consumption is obtained if annual, seasonal and geographic variations in the diet are included (Figure 5). Although estimates of consumption in individual years varied greatly, an apparent trend towards increased consumption of cod is present (Figure 5). From 1981 to 1988, consumption was similar to that predicted using the average diet. However, since 1989 estimates are generally greater than those obtained using the average. For two years (1990 and 1992) the estimated consumption was slightly above the upper 95% confidence intervals. The proportion of cod in the diet for both of these years was derived directly from reconstructed weights and not approximated from prevalence data.

Capelin Consumption

Estimates of total capelin consumption in the Gulf have increased from approximately 230,000 tonnes of capelin in 1981 to almost 445,000 tonnes (95% C.I. 208,000 - 727,000) in 1994 (Figure 6). In Newfoundland waters, it has risen from slightly over 321,000 tonnes to 620,000 tonnes (95% C. I. 288,000 - 1.0 million) between 1981 and 1994 (Figure 7).

Estimating annual capelin consumption incorporating seasonal and geographic effects on the diet, indicates that Newfoundland harp seals consumed large amounts of capelin in the early 1980s (e.g. over 850,000 tonnes in 1982), but that consumption declined by 1986 to approximately 490,000 tonnes. During the late 1980s and early 1990s capelin consumption has fluctuated around 600,000 tonnes.

Arctic Cod Consumption

Relatively small amounts of Arctic cod were consumed by harp seals in the Gulf (Figure 8), as expected from the distribution of this Arctic species. Consumption varied from 10,000 tonnes in 1981 to 20,000 tonnes in 1994. However, the variance associated with these estimates was large ranging from 0 to 48,000 tonnes in 1994.

More Arctic cod were consumed off Newfoundland than either of the other two species. An estimated 1.2 million tonnes (95% C.I. 73,000-1.7 million tonnes) were consumed in 1994. This is an increase of almost 50% since 1981 (Figure 9).

Using annual estimates of Arctic cod in the diet indicates that consumption was low in the early 1980s (35,000 tonnes in 1982) but increased to over 760,000 tonnes in 1986 (Figure 10). Consumption was estimated to have remained over 500,000 tonnes since the mid 1980s.

Discussion

This study presents preliminary consumption estimates of Atlantic cod, capelin and Arctic cod by harp seals inhabiting the Gulf of St. Lawrence, Southern Labrador Shelf and Grand Banks. These estimates are based on the assumptions that: total population size can be determined from the population model described in Shelton et al. (1995); energy requirements can be adequately estimated by the simple energy budget described; information on the seasonal distribution of animals is described by the distributions assumed in the model (Table 3); and that the stomach samples (Tables 4-6) accurately reflect the proportion of each prey species in harp seal diet. Each of these assumptions is discussed in detail below.

The estimates of population size used in this model were obtained from a population model incorporating age-specific reproductive rates, catch at age and independent estimates of pup production (Shelton et al. 1995). The estimates of the size and age structure of the population during the time period of this study depend upon the manner in which the mortality of pups is incorporated. Assuming that mortality is constant for all ages resulted in an estimates of 4.8 million (95% C.I. 4.1 - 5.0) harp seals in 1994. However, if the mortality of pups is greater than that of older seals, the point estimate may be as low as 4.5 million (Shelton et al. 1995). Although this represents only a change in abundance of 7%, the change in age structure of the population resulted in a 12% change in consumption.

The model is sensitive to the assumptions made when estimating the energy requirements of individuals. Changes in the 'growth premium' or 'activity factor' applied to the estimate of basal metabolic rate (BMR) affect estimates of total consumption. The lower growth premium reported by Olesiuk (1993) reduced the estimates of consumption by 7%. The energetic costs of activity, which have been estimated to range from 1.7 - 3 BMR (Worthy 1990), have a large impact on these estimates. Since this factor is a simple multiplier in the equation for energy requirements, changes in its assumed value are directly translated to changes in consumption. We used a conservative activity factor of 2 but altering this assumption could increase consumption by 50% or reduce it by 15%.

The estimates of energy requirements are also dependent upon the body mass used. In this model, we used the average body mass for harp seals during April. This is the month for which the largest sample sizes were available (Chabot et al. 1995). Harp seals undergo periods of weight gain to build up energy stores during the winter and subsequently lose weight during the breeding and moulting periods (Chabot et al. 1995). Therefore, energy may be gained in one area or season and used in another. April body weights, which are similar to those observed when seals arrive from the Arctic, are near the lowest for the period during which seals are present in northwest Atlantic waters and therefore, the energy requirements may be underestimated for the winter period and slightly overestimated for the summer period.

In this study we have used a relatively simple energy budget model to estimate individual energy requirements. Intuitively, a complex model incorporating seasonal changes in body mass and the costs of reproduction in energy requirements would appear to be more appropriate. However, the complex models require estimation of additional parameters making it more difficult to understand and can also introduce a false sense of increased precision since each additional factor is also measured with error. Recent studies indicate although the energy costs of reproduction may be high for breeding females, they increase total energy requirements of the population by only 5% (Olesiuk 1993; Hammill and Mohn 1994). Hammill and Mohn (1994) found little difference between estimates of Atlantic cod consumption by grey seals using a simple energy budget and a more complex one. Overall, our estimates of annual per capita energy requirements are intermediate to values estimated previously for harp seals by Lavigne et al. (1985) and Markussen and Oritsland (1991) using more detailed energy budget models.

Consumption of individual species are estimated as a proportion of the total consumption. Therefore, any changes in parameters affecting total consumption such as population size or energy requirements, will result in proportional changes in species consumption estimates.

Although estimates of consumption are sensitive to assumptions of population size and energy requirements, the potential range of changes in these parameters can be estimated. Unfortunately, the uncertainty associated with the seasonal distribution of harp seals is more difficult to determine. The proportion of energy obtained from each area was based on a distribution pattern obtained primarily from anecdotal information and tag returns. This information is biased because tag returns and observations are more common in populated coastal areas or in areas with a tradition of seal hunting. In addition, this information is difficult to quantify and does not provide insights into the offshore distribution of animals outside of the whelping and moulting periods. Fisher (1955) reported that the southward migration of harp seals may have been later in the 1950s than in the early 1920s. In contrast, there have been a number of anecdotal reports indicating that harp seals have migrated southward earlier in recent years and remained longer (Stenson, unpublished data). Such changes will affect any estimates of consumption by increasing (or reducing) the proportion of energy obtained in southern waters. This effect is likely to be important; changing the timing of the fall and spring migrations by a total of 1 month increased the estimate of consumption in Newfoundland and the Gulf by 12%.

Modifying the relative distribution of harp seals between Newfoundland and the Gulf of St. Lawrence, or between inshore and offshore areas, can also have a large impact on the consumption of individual prey species due to the geographical differences in the proportion of each species in the diet. For example, if additional energy is obtained from the Gulf, the higher proportion of cod and capelin in the diet would increase consumption estimates for these species while reducing that of Arctic cod. The same would occur if seals spent more time in offshore regions of Newfoundland. The deployment of satellite transmitters provides one approach in which the distribution of animals can be examined in detail. Studies on the movements of harp seals using satellite are currently underway with the release of 12 seals off Newfoundland in May/June 1995. Information from these animals, which will be monitored for up to one year, will provide new information on the distribution of harp seals throughout the year.

In order to estimate the consumption of individual prey species it is necessary to assume that the diet of the population is adequately described by the stomach samples available. Information on the diet composition of harp seals in the Gulf of St. Lawrence was limited to a few samples in the upper Estuary, the Magdalen islands during the breeding period, and the south and west coasts of Newfoundland. The samples from Newfoundland indicated that cod can form an important component of the harp seal diet, while the remaining samples from the Gulf indicate that insignificant quantities of cod are consumed. By using an average diet for Gulf harp seals, we assume that the amount of energy obtained in these different areas is proportional to the number of samples. For example, if Gulf harp seals spend the majority of their time in the estuary, these estimates of cod consumption will be too large but if they spend more time near Newfoundland, they will be underestimates. More information is required on what proportion of the population is found along the west coast of Newfoundland, central Gulf, or in the estuary, and the amount of time these animals spend in each of these areas.

The diet information available harp seals in Newfoundland waters was much more extensive and indicated that there was considerable variation in the diet among years, seasons and geographical areas. The average diet was heavily weighted towards nearshore samples in recent years (1990-1993) and contained equal numbers of winter and summer samples. In contrast, the annual estimates incorporate each of the diets separately weighting by season (according to Table 3) and the assumed nearshore/offshore distribution. This may account for the differences observed between the consumption estimates using the two methods. Since the nearshore samples used for the 'average' diet contained higher proportions of Arctic cod and less capelin than the offshore, the estimates obtained using the average diet indicate less capelin was consumed and more Arctic cod than those obtained using the annual estimates. The higher proportion of capelin (and less Arctic cod) the diet samples also indicates a decrease in capelin consumption (and increase in Arctic cod) since the early 1980s. Although it is often necessary to use diet information averaged over several years to obtain adequate samples, this may mask important trends in consumption which may occur.

The proportion of energy obtained from nearshore and offshore diets was assumed to be proportional to the geographical extent of the two areas. In the absence of information on the relative distribution of seals we had to assume that harp seals were randomly distributed throughout the area even though this is unlikely. Changes in this assumption can affect our estimates of consumption greatly. For example, if the proportion of energy obtained by harp seals in the offshore was decreased from 55% to 30% (54% reduction), estimates of Atlantic cod consumption would decrease by approximately 20%, capelin would decrease by 60%, and Arctic cod would increase by over 50% due to the different diets observed.

Estimated wet weights of prey ingested were not available for all years used in this study. Therefore, regressions were used to approximate the proportion of each prey species in the diet for years when only prevalence measures were available. This method provides only rough approximations of diet. Better statistical methods of estimating the proportion of the diet accounted for by each species in years for which only prevalence data are available must be developed.

The consumption estimates presented in this paper were restricted to the period 1981 to 1993 for which there were reasonably large samples available. It is possible to extrapolate back to 1965 when the population model begins. However, this would require assumptions concerning the nature of the diet which, given the variation observed over the time period of this model, may not be appropriate. To determine the impact of harp seal predation on commercial fish species, estimates of recent consumption are the most important, and is the time period for which we have the best data. Predicting future levels of consumption is difficult. The current rate of population growth may not be applicable if the recently observed reductions in reproductive rates continue (Sjare et al. 1995) and significant changes in the harvest levels of harp seals occur. Therefore, periodic estimates of pup production and monitoring of reproductive rates will be necessary in order to determine future population size. Also, the decline of capelin in the nearshore diet observed in the mid 1980's (Lawson and Stenson, 1995) and recent increase in the importance of herring in the diet illustrate the need to monitor diets on a regular basis in order to estimate the consumption of specific species.

Within the context of the above discussion, the consumption of major fish prey off Newfoundland has increased in recent years and is estimated to be in the order of 1.2 million tonnes (95% C.I. 735,000 - 1.7 million) of Arctic cod, 620,000 tonnes (95% C.I. 288,000 - 1.0 million) of capelin, and 88,000 tonnes (95% C.I. 46,000 - 140,000) of Atlantic cod in 1994. In the Gulf, harp seals consumed an estimated 445,000 tonnes (95% C.I. 208,000 - 727,000) of capelin, 20,000 tonnes (95% C.I. 0 - 48,000) of Arctic cod, and estimated 54,000 tonnes (95% C.I. 14,000 - 102,000) of Atlantic cod in 1994. The majority of the fish consumed are 10-20 cm in length (Lawson et al. 1994). These are primarily 1 and 2 year old Atlantic cod which are not recruited into the commercial fishery. The majority of capelin consumed are 1 and 2 year olds, with some 3 year olds which are also taken by the commercial capelin fishery. Attempts to assess the impact of harp seals on Atlantic cod stocks are beyond the scope of this paper. However, this study does indicate that harp seals are likely a major source of mortality for juvenile Atlantic cod, and an important predator on cod prey species. However, until our knowledge of seasonal distribution and annual, geographic, and seasonal variation in the diet are improved these estimates should be considered preliminary and used with caution.

Research Recommendations

In order to make significant improvements in our estimates of consumption additional research must be carried out. Quantitative information on the seasonal distribution of harp seals off the Newfoundland coast and in the Gulf of St. Lawrence must be obtained. This will require a concentrated satellite tagging effort. Monitoring of harp seal diet should be continued with expanded collection programs in the offshore and Gulf regions. Further research must be undertaken to determine biases in diet reconstructions and assimilation efficiency using captive and wild seals. Continued monitoring of the Northwest Atlantic harp seal population is required. However, considering the imprecise nature of surveys, the high expense, the complexity and difficulties associated with the analyses of aerial photographs, and the slow rate of change in population size, these surveys should be carried out periodically (3-5 years).

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Table 1: Mean body weights during April of harp seals of known age, for both sexes and from all years of collection (Chabot and Stenson 1995).

n	Age (yrs)	Weight (kg)
592	0	25.5
501	1	45.8
399	2	56.0
359	3	64.8
304	4	74.9
293	5	82.3
215	6	85.4
169	7	92.8
86	8	93.5
89	9	96.5
375	10+	101.8
Total = 3382		Mean = 65.0

Table 2: Increased energy required for growth (GF).

Age (yrs)	Lavigne et al. 1986	Olesiuk 1993
0	2.25	1.8
1	2.0	1.6
2	1.75	1.42
3	1.5	1.26
4	1.25	1.13
5	1.0	1.05
6+	1.0	1.0

Table 3: The proportion of annual energy obtained by harp seals from Newfoundland, Gulf of St. Lawrence and Arctic areas during 'Winter' (October - March) and 'Summer' (April - September) periods.

	Pups/Juveniles		Adults	
	Winter	Summer	Winter	Summer
Newfoundland	0.2355	0.1416	0.2939	0.1770
Gulf	0.0676	0.0368	0.0850	0.0460
Arctic	0.1956	0.3230	0.1197	0.2785

Table 4: Estimates of the total % wet weight of Atlantic cod, capelin and Arctic cod consumed by harp seals in the Gulf of St. Lawrence.

	Escoumins[1]	*Escoumins*[2]	Magdalen I.[3]	Nfld South Coast[4]	Nlfd West Coast[4]
Atlantic cod	1.00	-	-	13.77	13.19
Capelin	77.00	98.00	-	28.16	28.45
Arctic cod	-	-	-	0.07	10.12
Energy (kcal/g)	1.81	1.48	1.24	1.29	1.56
Sample size	25	9	62	126	241

[1] Samples collected January & February 1983; Murie and Lavigne 1991
[2] Samples collected *April 1988-1990*; Beck et al. 1993
[3] Samples collected March 1988-1990; Beck et al. 1993
[4] Samples collected November - June 1985-1993; Lawson and Stenson unpublished data

Table 5: Estimates of the total % wet weight of Atlantic cod, capelin and Arctic cod consumed by harp seals from Newfoundland during summer and winter.

		Nearshore						
	Prey Species	1982	1986	1990	1991	1992	1993	Offshore
Summer	Atlantic Cod	1.31	1.37	2.68	0.75	2.13	3.46	8.60
	Capelin	67.84	8.25	31.79	7.47	6.05	2.09	28.60
	Arctic Cod	5.1	74.67	42.24	40.43	34.95	41.08	0.55
Mean Energy Density (kcal/g)		1.27	1.31	1.41	1.47	1.57	1.35	1.30
Sample Size		88	101	71	77	60	47	160
Winter	Atlantic Cod	0.23	0.48	8.11	4.327	8.52	0.64	1.40
	Capelin	82.46	1.96	5.93	0.88	11.89	5.41	50.40
	Arctic Cod	2.68	87.31	61.38	68.04	58.94	77.14	2.00
Mean Energy Density (kcal/g)		1.42	1.03	1.30	1.29	1.28	1.30	1.40
Sample Size		202	442	172	117	158	57	112

Table 6: Mean and bootstrapped estimates of 95% confidence limits of % wet weights of Atlantic cod, capelin and Arctic cod in harp seal diets based on 14 samples from Newfoundland and 5 samples from the Gulf (Tables 5 & 6; 1,000 iterations).

Prey Species	Mean % Weight	Bootstrapped Mean %Weight	Lower 95% Confidence Limit	Upper 95% Confidence Limit
Newfoundland:				
Atlantic cod	3.14	3.17	1.69	4.85
Capelin	22.20	22.19	10.67	36.38
Arctic cod	42.60	42.67	27.25	57.56
Energy Density	1.35	1.35	1.31	1.40
Gulf:				
Atlantic cod	5.59	5.50	1.53	9.65
Capelin	46.30	45.06	23.60	69.00
Arctic cod	2.03	2.02	-	4.54
Energy Density	1.48	1.48	1.35	1.61

Table 7: Regression formulae used in reconstruction of percent weight estimates from prevalence (PR) measures for nearshore harp seals collected in Newfoundland during 1982-1993, in summer and winter.

	Regression Formula	N	r^2
Atlantic Cod	% Weight = 1.931 + (0.206 x PR) + (0.008 x PR^2)	24	0.885
Capelin	% Weight = 3.229 + (1.454 x PR) + (0.007 x PR^2)	21	0.613
Arctic Cod	% Weight = (1.133 x PR) - 0.978	16	0.763

Table 8: Estimated percent wet weights (% Wt) derived from prevalence measures for nearshore harp seals collected in Newfoundland waters during 1981-1989.

Season	Prey Species	1981	1983	1984	1985	1987	1988	1989
Summer	Atlantic Cod	-	3.21	-	2.07	4.65	2.69	6.15
	Capelin	-	50.12	17.32	49.92	30.67	31.32	24.5
	Arctic Cod	72.5	19.05	27.82	0.43	25.57	36.82	41.85
Sample Size		60	379	16	321	212	195	114
Winter	Atlantic Cod	5.03	2.83	1.92	4.69	2.81	2.65	3.86
	Capelin	7.03	58.03	57.61	4.49	4.28	13.92	21.39
	Arctic Cod	72.1	23.31	24.64	73.34	69.88	63.32	56.19
Sample Size		210	99	84	51	568	476	389

Table 9: Parameters used during initial and subsequent runs of the harp seal consumption model and the % change in estimated consumption in Atlantic waters.

Parameter	Initial Model Run	Alternate Model Runs	
		Parameters	% Change
1994 Total Population	4.8 million	4.5 million	- 12%
Activity Factor	2	2.5	+ 25%
Growth Premium	Lavigne et al. 1986	Olesiuk 1993	- 7%
Residency Period	Nov. 15 - June 15	Nov. 1 - June 30	+ 12%

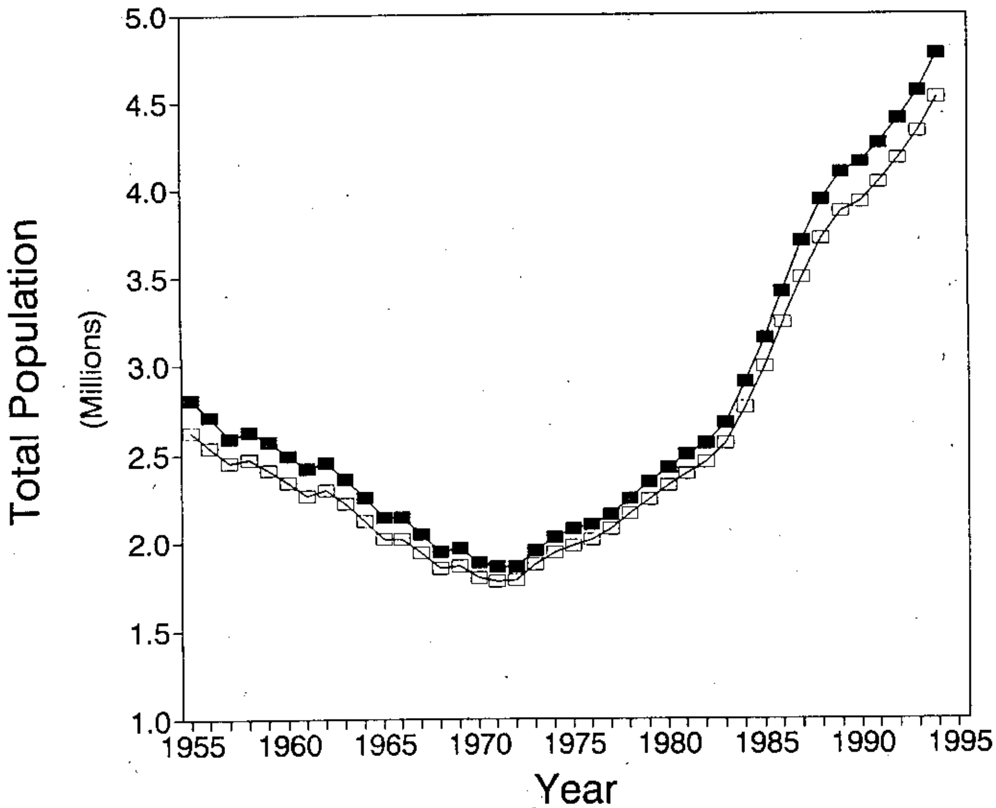

Figure 1: Abundance of northwest Atlantic harp seals assuming pup mortality is equal to that of adults (closed boxes) or 3 times that of adults (open boxes). From shelton et al. (1995).

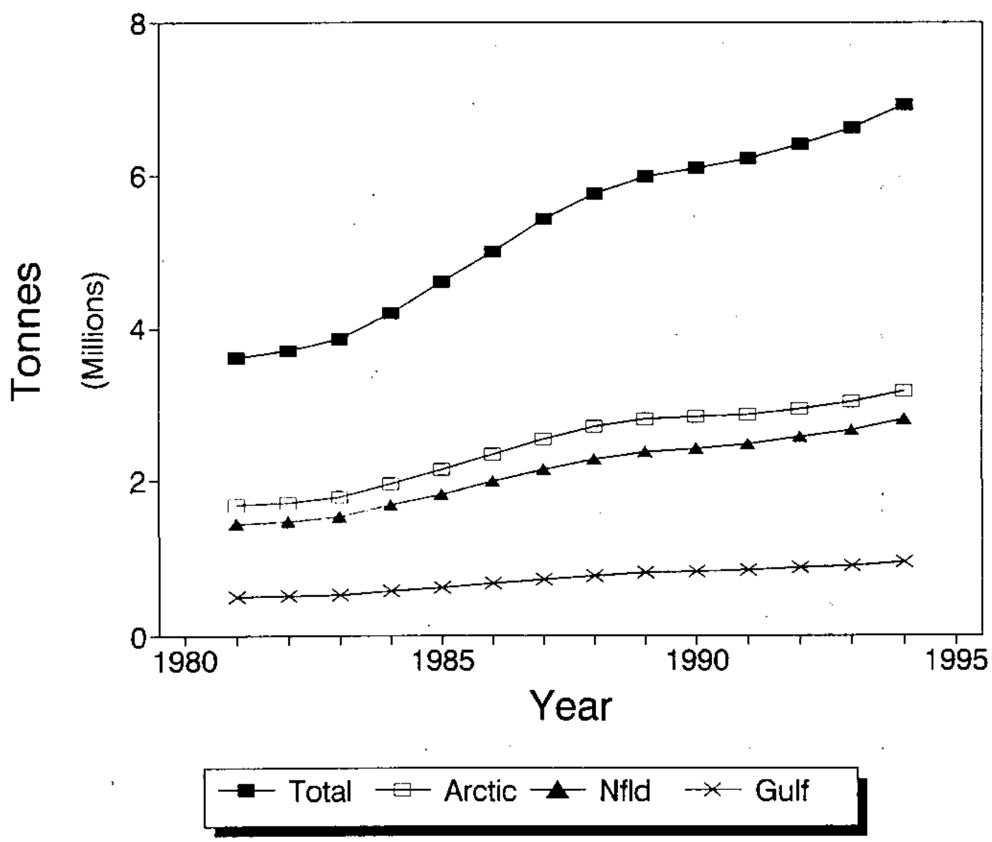

Figure 2: Total consumption of prey by harp seals in the northwest Atlantic.

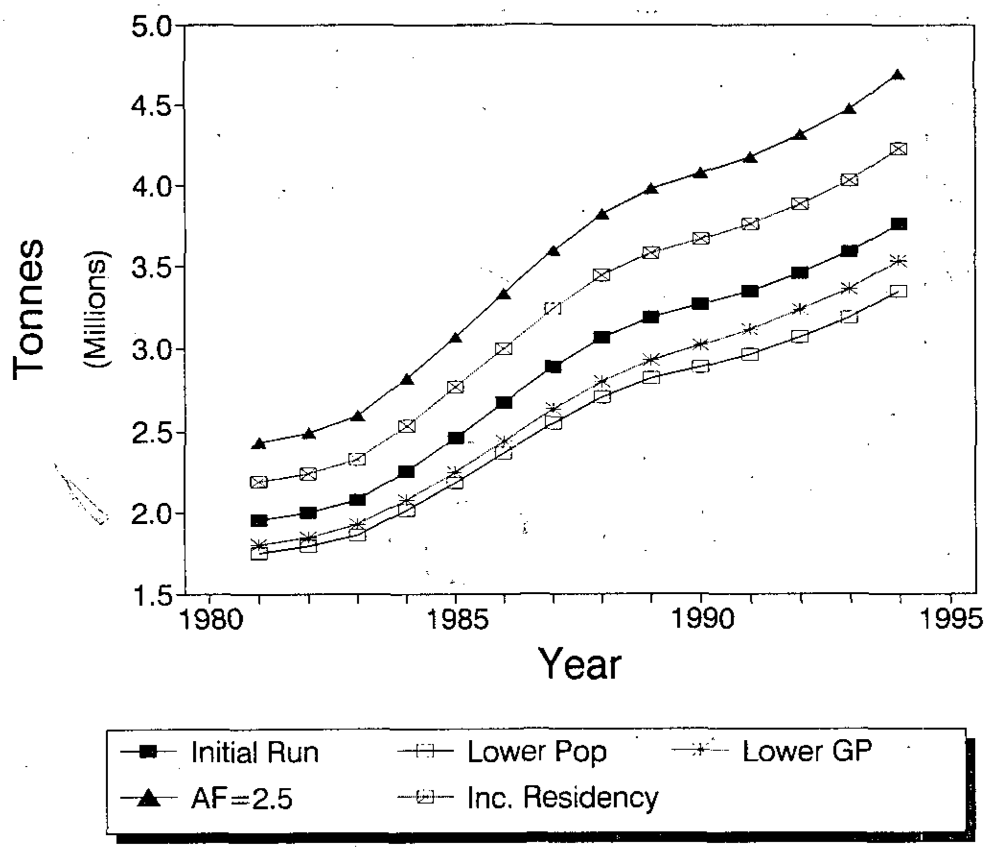

Figure 3: Estimates of prey consumption by harp seals in Newfoundland and the Gulf of St. Lawrence under differing assumptions. See Table 9 for a description of the parameters used.

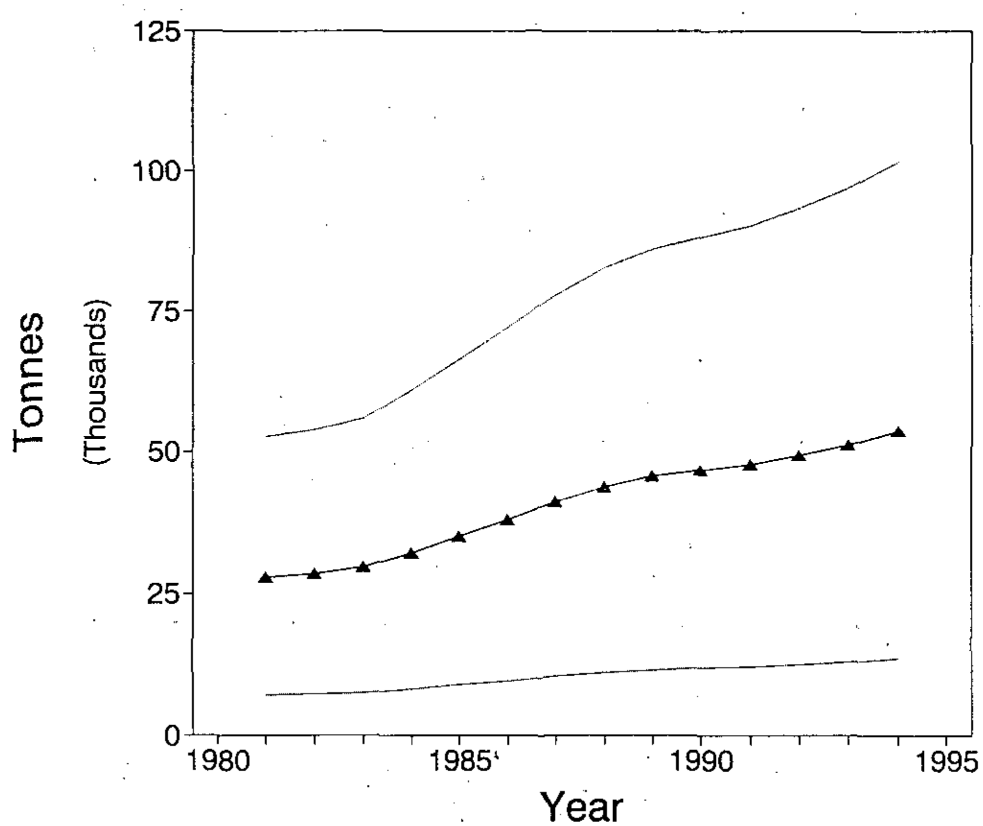

Figure 4: Estimated consumption of Atlantic cod in the Gulf of St. Lawrence using the average diet (and 95% C.I.).

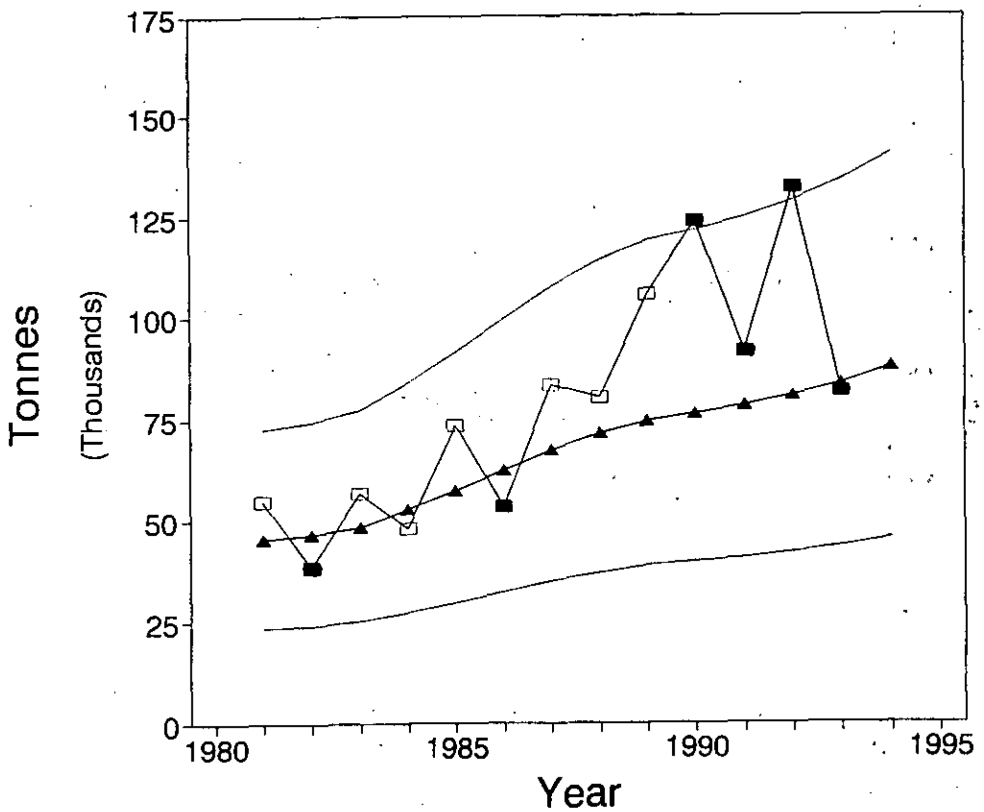

Figure 5: Estimated consumption of Atlantic cod in Newfoundland waters using average (triangles with 95% C.I.) and annual (boxes) estimates of the diet. Open boxes indicate years for which wet weights were approximated using prevalence.

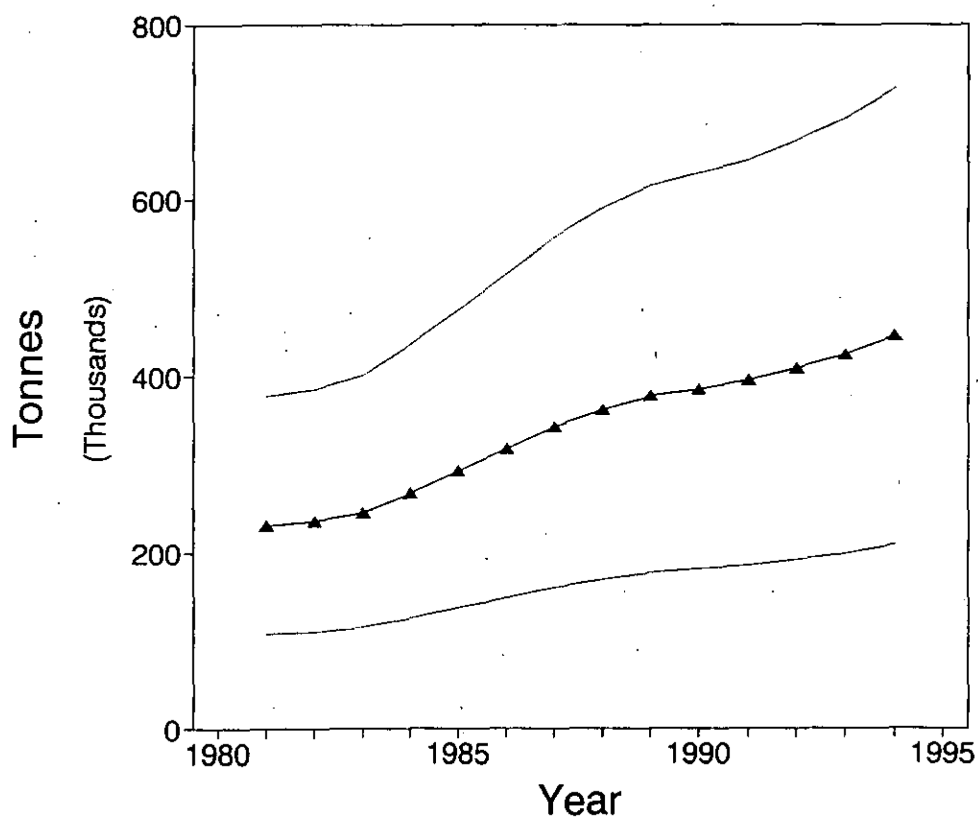

Figure 6: Estimated consumption of capelin in the Gulf of St. Lawrence using the average diet (and 95% C.I.).

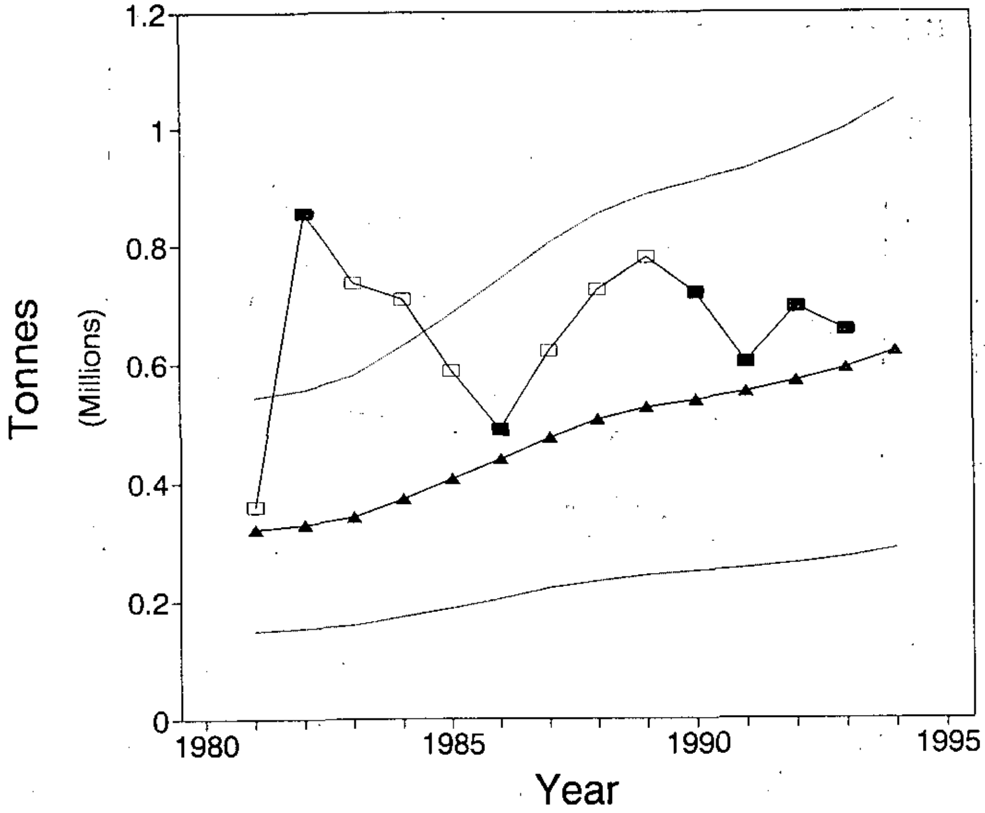

Figure 7: Estimated consumption of capelin in Newfoundland waters using average (triangles with 95% C.I.) and annual (boxes) estimates of the diet. Open boxes indicate years for which wet weights were approximated using prevalence.

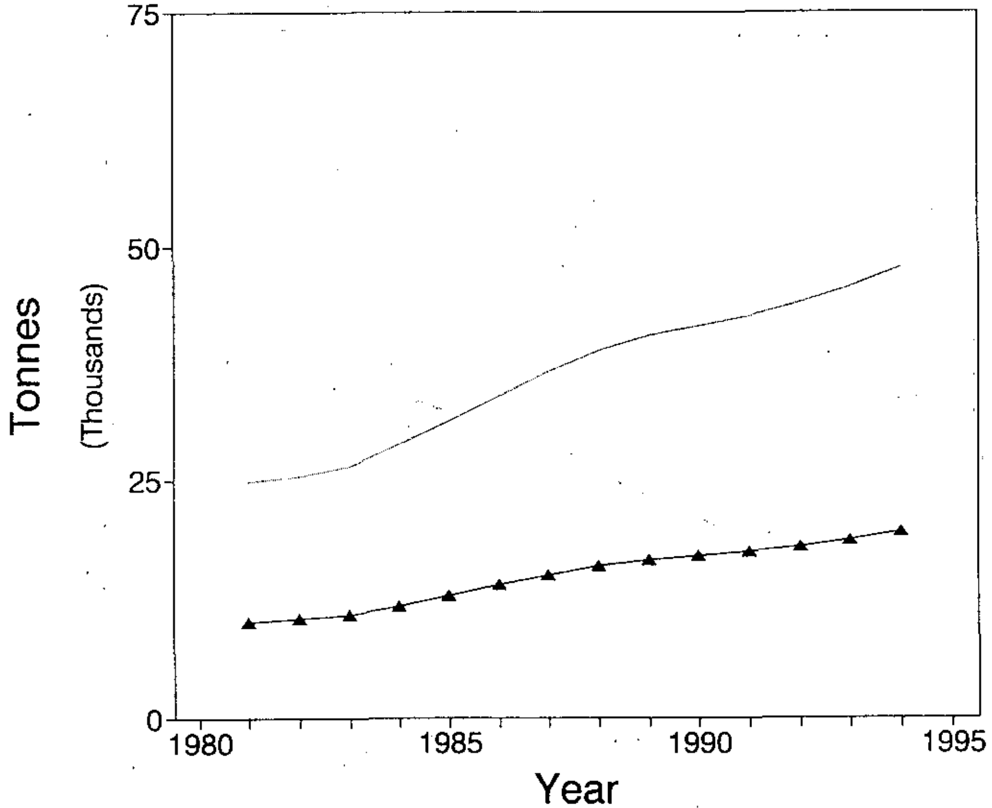

Figure 8: Estimated consumption of Arctic cod in the Gulf of St. Lawrence using the average diet (and 95% C.I.).

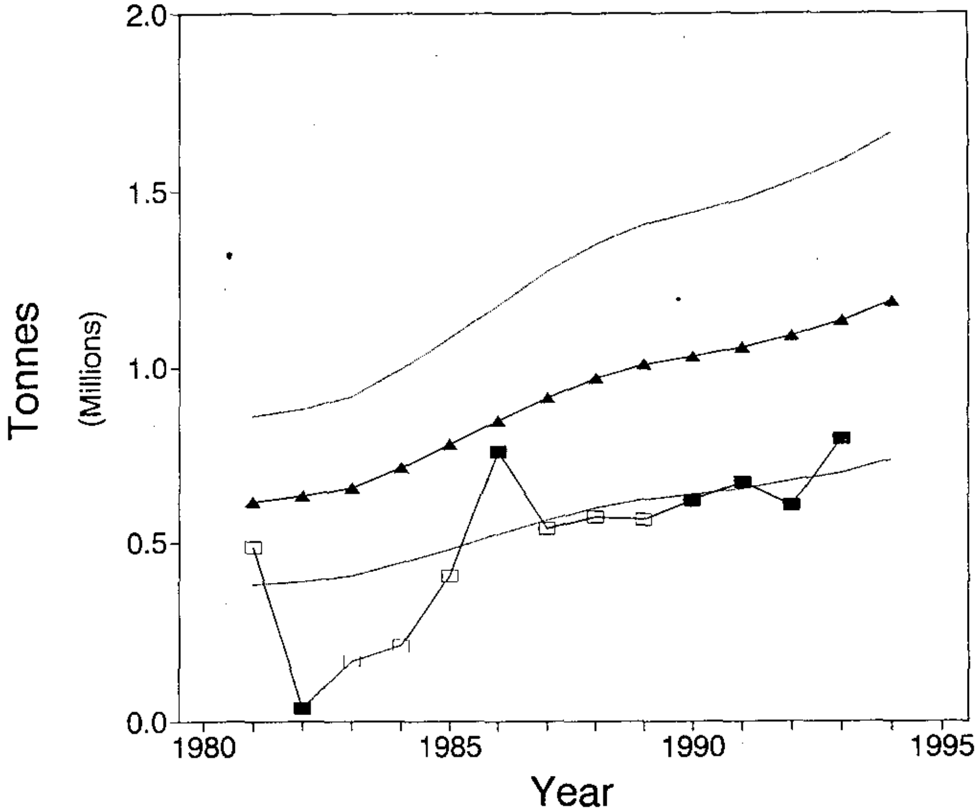

Figure 9: Estimated consumption of Arctic cod in Newfoundland waters using average (triangles with 95% C.I.) and annual (boxes) estimates of the diet. Open boxes indicate years for which wet weights were approximated using prevalence.