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A Model of grey seal predation on Atlantic cod on the Scotian Shelf and Gulf of St. Lawrence

by

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Abstract

Both the Sable Island and Gulf of St. Lawrence grey seal populations have increased substantially over the past several decades, such that total population size in eastern Canada in 1993 was estimated at about 143,000 animals. We extend a grey seal consumption model developed for 4VsW cod into four areas: 4VsW cod, Northern Gulf of St. Lawrence, Southern Gulf and an area called "Other" for the remainder of Atlantic Canada. Estimated total consumption of cod by grey seals in the four areas is estimated to have increased from < 6000 t in 1970 and may have increased to as much as 39,000 to 43,000 t in 1993, depending on model assumptions. Eighty percent of the cod consumed are pre-recruits to the commercial fishery.

Résumé

La population de phoques gris de l'Île de Sable et celle du golfe du Saint-Laurent ont toutes deux augmenté considérablement au cours des quelques dernières décennies, à un point tel qu'on estimait la population totale de phoques gris de l'est du Canada à environ 143 000 animaux en 1993. Nous avons appliqué un modèle de consommation de morue par le phoque gris dans 4VsW à quatre régions : 4VsW, nord du golfe du Saint-Laurent, sud du golfe et une zone désignée «autre», qui englobe le reste du Canada atlantique. On estime que la quantité totale de morue consommée par les phoques gris, qui était inférieure à 6 000 t en 1970, a augmenté, peut-être jusqu'à 39 000 à 43 000 t en 1993, selon les hypothèses inhérentes au modèle. La morue consommée se compose, dans une proportion de quatre-vingt pour cent, de prérecrues de la pêche commerciale.

Introduction

Grey seals are found throughout Atlantic Canada. In 1966, Mansfield (1966) estimated the total population to number around 5600 animals. Since then the population has increased and was thought to number around 84,000-110,000 animals in 1987 (Zwanenberg and Bowen 1990). This rapid growth has been accompanied by concerns that grey seals may have a negative impact on commercial fisheries through damage to fishing gear, transmission of parasites to commercially important fish species, or by consuming large quantities of important fish species (Malouf 1986).

Grey seals reproduce during December-February on land or on drifting pack ice. Two major whelping concentrations are recognized. An ice-breeding group located in St. George's Bay (Nova Scotia) and Northumberland Strait. A second larger colony is located on Sable Island. Other smaller whelping groups are found on Deadman Island near the Iles de la Madeleine in the Gulf and on small isolated islands located off the Nova Scotia eastern shore between Sydney and Canso. During much of the year animals from the various rookeries are believed to disperse widely, overlapping in their distribution (Mansfield and Beck 1977; Stobo et al. 1990; Lavigueur and Hammill 1993). On the whelping patch mixing between the two groups appears to be limited (Hammill unpublished data).

The decline in the east coast groundfish fishery has renewed concerns of the impact of seals on commercial fisheries. Recently, Mohn and Bowen (1994) developed a model to determine 4VsW cod consumption by grey seals and to evaluate the potential impact of grey seal cod consumption on the dynamics and potential yield of 4VsW cod.

The objective of this document is to extend the estimate of cod consumption by grey seals to other areas in Atlantic Canada. We have defined four areas for this study, which are 4VsW, the northern Gulf (4RS), and the southern Gulf (4T and including 4Vn). The remaining areas, which include zones 3P, 4X and 2J3KL have been grouped into a category known as Other. Two approaches have been followed. In the first approach the age structured seal and fish consumption model (Model 1) developed by Mohn and Bowen (1994) is extended to grey seals in the Gulf of St. Lawrence and other areas incorporating appropriate information on seal distribution (Clay and Nielsen 1985; Lavigueur and Hammill 1993) and diet (Benoit and Bowen 1990; Murie and Lavigne 1992; F. Proust and M. Hammill unpublished data). The second approach, is very similar with the exception that the simple energy budget developed by Mohn and Bowen (1994) is replaced by a more detailed energy budget (Model 2) which attempts to estimate grey seal energy requirements over time taking into account seasonal factors such as reproduction, and moult.

Methods

Seal Population Model

Zwanenburg and Bowen (1990) used a Leslie matrix to model both the Gulf and Sable Island grey seal populations in eastern Canada. They assumed that grey seals lived to a maximum age of 34 years and that males and females had the same natural mortality rates. Mohn and Bowen (1994) built on the approach used by Zwanenburg and Bowen (1990) by constructing a deterministic, age-structured model similar to a Leslie matrix model that assumes different rates of natural mortality in males and females after age 5 and different rates for the Gulf and Sable Island components of the population. In the model, all seals are assumed to die at 40 years of age. A two parameter model for each herd was then fit to pup production estimates from the Gulf of St. Lawrence (Hammill et al. 1992) and Sable Island (Stobo and Zwanenburg 1990; Zwanenburg and Bowen 1990; Mohn and Bowen 1994).

Seasonal Distribution of the Grey Seals

Seasonal distributions of each of the herds have been inferred from tagging studies, and aerial observations (Clay and Nielsen 1985; Mansfield and Beck 1977; Stobo et al. 1990; Lavigueur and Hammill 1993)(Table 1). For the most part, outside of the distribution of adults on the whelping grounds, quantitative information on the distribution of animals is not available. For the Sable Island herd, 90% of the animals were assumed to be in 4VsW during the first quarter (January-March). April-June are considered to be a dispersal period (Stobo et al 1990), consequently 50% of the animals were assumed to remain in 4VsW, 25% moved into the Gulf, and the remaining 25% were dispersed throughout other areas (4X, 3Pn etc). During the third quarter, animals were still assumed to be widely dispersed with 50% of the Sable herd still found in 4VsW, 15% in the Gulf of St. Lawrence and the remaining 35% in the Other zones. During the final quarter (October-December), 80% of the herd was located in 4VsW, 5% in the Gulf and 15% in other regions (Table 1). For the Gulf grey seal herd, during the first quarter 70% of the animals were assumed to be in the southern Gulf, and the remaining 30% were assumed to be distributed evenly between the Northern Gulf, 4VsW, and Other. For the remainder of the year, tag returns and aerial observations (Stobo et al. 1990; Lavigueur and Hammill 1993; Clay and Nielsen 1985) suggested two quite different distribution patterns. Consequently, consumption was estimated assuming two different distributions for the Gulf herd during the remainder of the year. In the first scenario, the tagging data suggested that the seals were evenly distributed between the northern and southern Gulf during the second and third quarters. For these two quarters, 20% of the herd was located in 4VsW, 35% in the Northern Gulf, 35% in the southern Gulf, and 10% were located in Other. For the fourth quarter, 70% of the animals were assumed to be in the southern

Gulf, and the remaining 30% distributed evenly between the northern Gulf, 4VsW, and Other (Table 1). The aerial survey data (Clay and Nielsen 1985) suggested that more animals were located in the northern Gulf than in the southern Gulf, consequently for the second scenario, 60% of the animals were assumed to be in the Northern Gulf, 10% in the southern Gulf, 10% in Other and 20% in 4VsW. During the fourth quarter, 50% were assumed to be the Northern Gulf, 30% in the Southern Gulf, 10% in 4VsW and 10% in Other.

The Predation Model and Seal energy requirements

The estimation of seal energy requirements followed two approaches. The first approach extended the model (Model 1) developed by Mohn and Bowen (1994) to the whole Northwest Atlantic grey seal population. In this model, energy requirements are assumed to be constant throughout the year. Individual energy requirements were calculated using an allometric relationship linked to mass at age data, and including a correction for the additional energy requirements associated with growth. Total energy requirements were estimated by multiplying individual energy requirements by the number of seals in each region and summing these over each quarter.

In the second case (Model 2) an attempt is made to model energy requirements of grey seals (Hammill and Ryg unpublished), taking into account seasonal changes in energy requirements including moult and reproduction. Model 2 is implemented as a spreadsheet using Microsoft Excel, where energy requirements are calculated on a daily basis and summed over quarterly periods. The basic inputs are sex (male, pregnant females and non-pregnant females) and age. For each day, the energy requirements for basal metabolic rate, growth, reproduction and activity are calculated. The sum of BMR and activity is compared with the minimum heat required for thermal stability and the largest of the two values is set as the maintenance requirement. To this net energy is added an "apparent" heat increment of feeding (HIF). This apparent heat increment of feeding is the heat increment of feeding minus the difference between the minimum heat production for thermal stability and the sum of BMR and activity. The model is driven by body mass and fat content. Body mass is calculated from a Gompertz growth equation (Hammill unpublished data). Seasonal changes are implimented by splitting the year into periods of breeding, molting, fat buildup and winter. Total growth rates and changes in lean mass and sculp weights are adjusted to fit observed seasonal changes from biological data. Pup growth in mass and changes in body composition during lactation and female mass loss follow Baker et al. (In press). The duration of male mass loss during the breeding season was set assumming that males lose 25% of their mass. The rate of mass loss followed the regression of Anderson and Fedak (1985), which is similar to the rates of mass loss observed in males on the whelping patch (Tinker 1993). During the breeding season, adults are assumed to spend 80% of their time on the ice, with a Kleiber factor of 2 and 4 for females and males respectively. The remaining time was spent searching in the water with a Kleiber factor of 2.5. During the molt animals are assumed to spend 95% of their time on land with a metabolic rate of 1.62 x Kleiber corresponding to a decrease of 19% from 2 x Kleiber (Ashwell-Erickson et al. 1986). The remaining 5% of the time was spent searching with a Kleiber factor of 2.5. During cruising or searching the Kleiber factor was set to 2.5. Outside of the breeding or molt period the activity budget was set as 13 % hauled out, 41% resting, 32% cruising, and 14% of the time was spent searching (Thompson et al 1991). The Kleiber factors during haulout and rest outside of the breeding season were set at 1.66. For energy requirement calculations the year was divided into equal quarters (Jan-March, Apr-June, July-Sept, Oct-Dec) to allow comparison with Mohn and Bowen (1994).

Prey size and composition of grey seal diets

Diet information for the Northern Gulf came from published sources (Murie and Lavigne ; Benoit and Bowen 1990), and more recent collections from Anticosti Island (Proust and Hammill, unpublished data).(Table 2). Diet composition was determined by identification of hard parts in stomach. Diets were reconstructed using otolith-length or weight relationships. Since not all items consumed are identified or can be reconstructed we assumed that 20% of the diet with a caloric value of 0.8kcal/g was not accounted for and adjusted the reconstructed diets accordingly. Diet information for 4VsW was available from Mohn and Bowen (1994).

Bootstrap samples were drawn from the northern Gulf and 4VsW samples (Mohn and Bowen 1994) to determine a mean diet for the northern Gulf and 4VsW areas respectively (Tables 3, 4). Bootstrapping (Efron, 1982) is a computer intensive technique in which the
underlying data are resampled, the analysis repeated and the results compiled. We have 13 estimates seal diets for 4VsW and 4 for the Northern Gulf. Our bootstrapping procedure resampled with replacement the 13 or the 4 possible diets to produce a mean percent cod and mean energy density of the diet for each quarter of the simulation. This procedure was repeated 100 times and the cod consumptions compiled so their modes and 95% confidence limits estimated. Shown in Fig. 2 are the 95% error limits in cod consumption for the two areas for which we had data. In either case the coefficient of variation was about 10%.

Diet information from the southern Gulf is limited to 4 stomachs from the Magdalen Islands and 11 stomachs from Amet Island. No information on diet is available for grey seals from the western Gulf and from 4Vn on the Cape Breton east coast. Similarly, diet information for area Other (4X, 3Pns, 2J3KL etc) are not available or are very limited. For these samples we assumed that cod comprised 10% by weight of the diet and the average energy density of the diet was 1.5 kcal/g.

Cod consumption by size class was estimated by dividing the size ranges into <30 cm, 31-45 cm and >45 cm. Forty-four percent of the fish consumed were <30 cm, 36% were 31-45 cm in length and 20% were >45 cm. These sizes were meant to correspond to early pre-recruits, fish near recruitment by the industry and fish that are fully recruited.

Results

Population

The 1993 Gulf population was estimated at 61,900 animals with a doubling time of about 8 years. The 1993 Sable Island component was estimated to be 81,600 animals and is doubling at a rate of around 6 years (Mohn and Bowen 1994)(Figure 1).

Energy consumption

Total energy consumption differed between the two models by less than 1%. While Model 1 assumed that energy consumption was evenly distributed throughout the year, Model 2 indicated that 19.8%, 22%, 30.2%, and 27.8% of the energy consumed occurred in quarters 1 to 4 respectively.

Estimated cod consumption by grey seals was 38,500 to 43,300 tonnes in Atlantic Canada in 1993, depending on the model and distribution of animals in the Gulf used. Broken down into size classes, cod consumption would be 17,000-19,000 tonnes of cod <30 cm, 13,700-16,000 tonnes of 31-45 cm cod and 7,600-8,600 tonnes of cod >45 cm. Assuming that cod consumption by grey seals followed the pattern described by a demand model then cod consumption has increased from <6000 t in 1970 to 43000 t in 1993 (Table 6,7; Fig. 2-5). Estimates of cod consumption using Model 1 (Mohn and Bowen 1994) were approximately 2% higher than cod consumption estimates obtained from Model 2. Cod consumption was greatest in 4VsW at around 17,000 tonnes, and has shown the greatest change over time (Figures 2-5). The change in the 4VsW consumption curve over time has also been quite smooth reflecting its dominance by the Sable herd which has grown at a constant rate since 1970. Cod consumption by grey seals in the two Gulf areas has also increased over time. The discontinuity in the curve in the early 80s is due to the effects of a government cull on the whelping patch at this time.

As expected cod consumption in the Gulf of St. Lawrence was seriously affected by the distribution of animals. Using distribution 1, cod consumption in the Southern Gulf was approximately 58% of the Northern Gulf consumption (Table 6,7; Figure 2-5). However, under the scenario of the second distribution where the majority of grey seals during the third and fourth quarters are in the northern Gulf, cod consumption in this area approaches 17,000 tonnes, similar to the levels observed in 4VsW cod, while Southern Gulf consumption decreases to about 28% of Northern Gulf consumption.

Discussion

This study represents a first attempt at synthesizing available information on diet, population size and distribution of Gulf of St. Lawrence and Sable Island grey seals to estimate cod consumption in 4 zones in Atlantic Canada. It indicates that total cod consumption in Atlantic Canada is in the neighbourhood of 38,500-43,300 tonnes of cod, 80% of which consists of pre-recruits to the commercial fishery. Over subsequent months it is likely that these estimates will change as the models are refined and new information is incorporated into the models.

In arriving at these estimates we have made the following assumptions in our model:
1) the Northwest Atlantic population has been increasing at an exponential rate since 1970;
2) diets used in Tables 2 and 3 accurately reflect the proportion of cod in grey seal diets;
3) the seasonal distribution of grey seals can be described by the distributions outlined in Table 1;
4) grey seal energy requirements can be adequately described by either of the energy budget models;
5) the functional form of seal/cod interactions can be described by a demand model.

In our preliminary analysis we have not attempted to examine the effects of uncertainties in our assumptions on our model output. Mohn and Bowen (1984) examined the effects of a 10% change in model parameters on estimates of 4VsW cod consumption. In their analysis a 10% increase in the size of the Sable Island herd, proportion of cod in the diet, size at age, and the Klieber multiplier increased the proportion of cod in the diet by 10%, while a 10% increase in Metabolizable energy decreased consumption by 11%. However, 10% changes in the proportional distribution of animals in 4VsW, the proportion of unseen prey, and the heat increment of feeding altered consumption estimates by <3%.

The above analysis examined the effects of 10% changes in model parameters. However some further discussion of these assumptions and the confidence that can be placed in each assumption is warranted.
1) We have assumed that the grey seal population has increased (and is continuing to increase) at an exponential rate. At some point density-dependent changes in population parameters will alter population trajectories, but recent information on reproductive parameters do not indicate that such changes are yet occurring (Hammill unpublished data). For the Sable Island herd current

information indicates that the population as indicated by changes in pup production have increased exponentially during the period 1977-1993. In the Gulf, there is much greater uncertainty surrounding population estimates, due to a lack of information on population size over time and the possibility of more variable pup mortality rates associated with this ice breeding herd. Although we have presented changes in the population since 1970 including the effects of a government cull of this herd during the 1970's and 1980's, these estimates are extrapolations using pup production estimates available for 1984-1990.

2) Diets used in Tables 2 and 3 accurately reflect the proportion of cod in grey seal diets. Species composition in marine mammal diets are largely determined by identification of hard parts in stomachs or faeces. Some of the difficulties associated with this approach are discussed by Mohn and Bowen (1994). Quantitative information on grey seal diets in eastern Canada are available for some areas since 1983 (Northern Gulf) and for other areas such as Nova Scotia since 1988. Although these samples suggest that there is some seasonal and interannual variability in the fraction of cod in the diet, sample sizes are too small to provide a more complete analysis throughout the study period. Consequently, we have assumed that cod consumption does not change thoughout the year and have attempted to evaluate some of the uncertainty in this assumption by bootstrapping the proportion of cod in the diet and mean energy density to provide confidence intervals for 4VsW and Northern cod consumption. Unfortunately, for much of the grey seal's range including the southern Gulf, east coast of Cape Breton Island, 2J3KL and 3Psn, and the Bay of Fundy, quantitative diet information is limited or lacking completely. For some of these areas, there is some qualitative diet (frequency of occurrence) information available, but this index tends to underestimate the importance of cod in the diet relative to percent weight (Benoit and Bowen 1990). For the southern Gulf and "Other", we have assumed that cod comprises 10% by weight and an average energy density of of the diet of 1.5 kcal/g. This assumption lies at the lower end of the range of 6%-46% and 1.2-2.1 kcal/g seen in other studies (Mohn and Bowen 1994; Hammill unpublished data). Frequency of occurrence data from the southern Gulf indicate that cod was found in 13.6% of a sample of 89 stomachs (Benoit and Bowen 1990) suggesting that our assumption of 10% cod in the diet is not unreasonable.

3) The seasonal distribution of grey seals can be described by the distributions outlined in Table 1.

Our estimates of cod consumption changed markedly with changes in assumed seasonal distribution of animals in the Northern Gulf owing to the higher fraction of cod in grey seals in this area. As outlined earlier, outside of the whelping period when virtually all breeding animals are concentrated around two major whelping areas, quantitative information on the seasonal distribution of grey seals is not available. Current information on distribution has been obtained from tag returns and in the Gulf from aerial surveys. Tag return information is of limited use because hunting effort cannot be quantified throughout Atlantic Canada (Stobo et al 1990; Lavigueur and Hammill 1993). Animals on Sable Island have not been subject to a bounty hunt, while along the Nova Scotia eastern shore animals were hunted for bounty. In the Gulf there was little knowledge of the bounty on the Gaspe, southwestern and southern Newfoundland coasts. Extensive hunting for bounty occurred in the southern Gulf, Magdalen Islands and during the summer on Anticosti Islands, although in the latter case some of this hunting occurred in conjunction with scientific collections carried out at the same time. Animals were also protected during January to March in the Gulf and May to September in the estuary. Although much of the information involved in estimating cod consumption by Atlantic grey seals is likely to be refined over the coming months (reproductive rates, diet, size at age), quantitative information on the seasonal and geographic distribution of grey seals in the different regions will not be available in the near future. Using visual aerial surveys to count hauled out animals may provide some information on relative distribution throughout their range (Clay and Nielsen 1985). However, this approach will not provide information on whether a hauled out animal is of Gulf of St. Lawrence or Sable Island origin. Additional information is required on the fraction of animals located in inshore vs offshore regions and the proportion of animals hauled out on land vs animals in the water, before this approach can be developed further. Further advances in this area will require an increased effort in the deployment of satellite and time depth recorder telemetry.

4) Grey seal energy requirements can be adequately described by an energy budget model. Two models were developed to estimate energy requirements of grey seals. Although both models linked energy requirements to mass at age and both models were based on age-weight data from the Northern gulf, model development occurred independently. Surprisingly, little difference was observed in the predicted energy requirements and consequently cod consumption estimates between the 2 models. In Model 1, it was assumed that annual energy requirements could adequately be described by an allometric equation and field measurements suggest that this assumption is not unreasonable. There is some uncertainty about the growth premium needed to account for the higher metabolic rate of juveniles, but our assumed growth premiums are somewhat lower than suggested premiums in the literature (see Mohn and Bowen 1994) and could easily be modified as new information becomes available. Seasonal variations in energy requirements associated with reproduction, the moult, changes in body mass and activity were explicitly not accounted for in this model. Failure to include the costs of reproduction results in approximately a 5% underestimate in population energy requirements of harbour seals (Olesiuk 1993). Activity was not included owing to the lack of time budget information for grey seals for much of the year. Since body mass undergoes significant annual changes, estimates of energy requirements from this model are obviously sensitive to changes in this parameter. Body masses used to calculate energy consumption in Model 1 were based on data collected during July and August, when

body mass is approximately 85% of the maximum mass observed during January (Hammill unpublished data). Model 2 attempted to model more closely the seasonal changes in energy requirements owing to changes in body mass, the effects of reproduction, and incorporated available information on activity. Although intuitively this approach may appear to be more appropriate, the incorporation of additional factors increases model complexity and may give a false sense of model precision since each additional parameter is also measured with error. Examination of the additional costs of reproduction in Model 2 indicated that reproduction did result in a 5% increase in energy requirements at the population level. Also, seasonal changes in energy consumption were observed, with 19.8 and 22% of the energy consumption occurring in the first 2 quarters and 30.2% and 27.8% of the annual energy consumption occurring during the last two quarters. In the present exercise, failure to incorporate seasonal changes in energy consumption into the annual energy budget is not thought to have a major effect on overall cod consumption estimates since diet composition was not allowed to vary seasonally. This may also not be a factor in estimating cod consumption (vs consumption of other species eg capelin) if annual movements of grey seals track the annual movements of their prey.
5) the functional form of seal/cod interactions can be described by a demand model. For this analysis we chose a demand model to describe the functional form of the interaction between seal and cod for the analysis of potential impacts of seals on cod; ie we have assumed that on average seals will find a certain amount of cod irrespective of its relative abundance. Because the seal population varied by about a factor of ten over the period of investigation the cod consumption is dominated by seal abundance. This model is of course less likely as the amount of cod compared to other prey species decreases to very low levels while seal herds increase. Unfortunately for most prey items, there are neither assessments nor in many cases even reliable survey estimates. Until supporting data become available any model chosen will be rather speculative and sensitivity to assumptions about form would be the most profitable analysis. Despite uncertainties in the data over the period covered by the model, the strength of our study is that extensive data on both population size and diets were collected during the most recent period (1983-1992) and little extrapolation is required to assess the current situation. It is only when we attempt to project backwards prior to 1980 or beyond 1992, that the form of the applied model becomes more important.

Within the context of the above assumptions, this analysis suggests that cod consumption has increased to around 38,000 to 43,000 tonnes in Atlantic Canada. Although much of this consumption occurs in 4VsW, the estimates of cod consumption by region must be considered to be preliminary since the seasonal and geographic coverage of diet samples throughout the grey seal's range and quantitative information on the seasonal distribution of animals are limited.

Much of the cod consumption by grey seals consists of pre-recruits to the commercial fishery. From the diet reconstructions grey seals in Atlantic Canada would consume 15,000-20,000 tonnes of <30 cm cod, 13,000-16,000 tonnes of 31-45 cm cod and 7,000-9,000 tonnes of >45 cm cod. Attempts to assess the impact of grey seal cod consumption on cod stocks are beyond the scope of this paper. Although grey seals consume large numbers of small cod (pre-recruits), which represents a significant potential loss to the industry, it is also likely that some compensatory mortality occurs which would reduce this impact.

Since harp, harbour and hooded seals are also found off Newfoundland and in the Gulf of St. Lawrence, our estimate of cod consumption by grey seals represents only part of total cod consumption by seals. Unfortunately, no information is available on harbor seal populations in the Gulf and Newfoundland. However, hooded seals were sureyed in 1990, and a recent survey to estimate harp seal pup production was completed in March 1994. Results from this survey are expected by early 1995. With this information along with recent diet information it should be possible to extend this analysis of cod consumption to harp and hooded seals.

Research Recommendations

One of the benefits of this exercise has been to highlight gaps in our existing knowledge. It is evident that continued monitoring of grey seal populations and diet from Sable Island and the Gulf are required to determine if the seal population is continuing to expand exponentially and to determine if the fraction of cod in the diet changes in relation to cod or seal abundance. More information is required on grey seal diets throughout the year, particularly in the southern Gulf and on the Scotian Shelf, from areas where current data is very limited or non-existent. This information is important, and much of it can be collected as part of ongoing programs. However, in order to make significant improvements to our estimates, quantitative information on the seasonal distribution of grey seals is required. Although it may be possible to obtain some of this information from aerial surveys, most of the required information can only be obtained via a major telemetry study (satellite transmitters and time depth recorders). Using this approach it will be possible to work out the proportion of animals hauled out, in coastal vs offshore areas and finally the seasonal distribution of animals within the different fish zones in Atlantic Canada.

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Table 1. Distribution of each population of grey seals over the 4 areas by quarter of year. The first quarter begins 1 January. Two different distributions were examined for the Gulf herd.

Sable Island herd

	1st Q	2nd Q	3rd Q	4th Q
4VsW	0.9	0.5	0.5	0.8
N Gulf	0	0.125	0.075	0.05
S Gulf	0	0.125	0.075	0
Other	0.1	0.25	0.35	0.15

Gulf herd distribution 1

	1st Q	2nd Q	3rd Q	4th Q
4VsW	0.1	0.2	0.2	0.1
N Gulf	0.1	0.35	0.35	0.1
S Gulf	0.7	0.35	0.35	0.7
Other	0.1	0.1	0.1	0.1

Gulf herd distribution 2

	1st Q	2nd Q	3rd Q	4th Q
4VsW	0.1	0.2	0.2	0.1
N Gulf	0.1	0.35	0.6	0.5
S Gulf	0.7	0.35	0.1	0.3
Other	0.1	0.1	0.1	0.1

Table 2. Grey seal diets from the northern Gulf of St. Lawrence.

Season	N	Mean energy density (kcal/g)	% wt cod	Source
May-Aug 1988	114	1.73	0.16	Proust & Hammill unpublished
July-Aug 1986-87	184	1.35	0.41	Benoit and Bowen 1990
Aug-Sept 1992	100	1.42	0.46	Proust & Hammill unpublished
Jul-Dec 1983	44	1.61	0.36	Murie & Lavigne 1992

Table 3. Bootstrapped mean percent by weight cod in grey seal diets after correcting for unidentified prey.

Region	1st Q	2nd Q	3rd Q	4th Q	Source
4VsW	12.8	12.8	12.8	12.8	Mohn & Bowen 1994
N Gulf	28.1	28.1	28.1	28.1	Table 2
S Gulf	8.3	8.3	8.3	8.3	Assumed
Other	8.3	8.3	8.3	8.3	Assumed

Table 4. Bootstrapped mean energy density (kcal/g) in grey seal diets after correcting for unidentified prey.

Region	1st Q	2nd Q	3rd Q	4th Q	Source
4VsW	1.42	1.42	1.42	1.42	Mohn & Bowen 1994
N Gulf	1.41	1.41	1.41	1.41	Table 2
S Gulf	1.38	1.38	1.38	1.38	Assumed
Other	1.38	1.38	1.38	1.38	Assumed

Table 5. Comparison in annual and seasonal energy intake between Model 1 and Model 2 using the estimated 1993 grey seal population.

Model 1

Population	Annual total	1st Q	2nd Q	3rd Q	4th Q
Sable Males	1.23E+11	3.08E+10	3.08E+10	3.08E+10	3.08E+10
Sable Females	1.23E+11	3.08E+10	3.08E+10	3.08E+10	3.08E+10
Sable Total	2.46E+11	6.16E+10	6.16E+10	6.16E+10	6.16E+10
Gulf Males	9.81E+10	2.45E+10	2.45E+10	2.45E+10	2.453E+10
Gulf Females	8.38E+10	2.10E+10	2.10E+10	2.10E+10	2.096E+10
Gulf Total	1.82E+11	4.55E+10	4.55E+10	4.55E+10	4.549E+10
Model 1 Total	4.28E+11	1.07E+11	1.07E+11	1.07E+11	1.07E+11

Model 2

Population	Annual total	1st Q	2nd Q	3rd Q	4th Q
Sable males	1.18E+11	2.64E+10	2.59E+10	3.32E+10	3.26E+10
Sable females	1.24E+11	2.46E+10	2.75E+10	3.77E+10	3.46E+10
Sable Total	2.49E+11	4.92E+10	5.50E+10	7.53E+10	6.92E+10
Gulf males	9.34E+10	2.10E+10	2.04E+10	2.60E+10	2.59E+10
Gulf females	8.27E+10	1.69E+10	1.82E+10	2.44E+10	2.32E+10
Gulf Total	1.76E+11	3.38E+10	3.64E+10	4.87E+10	4.65E+10
Model 2 Total	4.25E+11	8.30E+10	9.14E+10	1.24E+11	1.16E+11

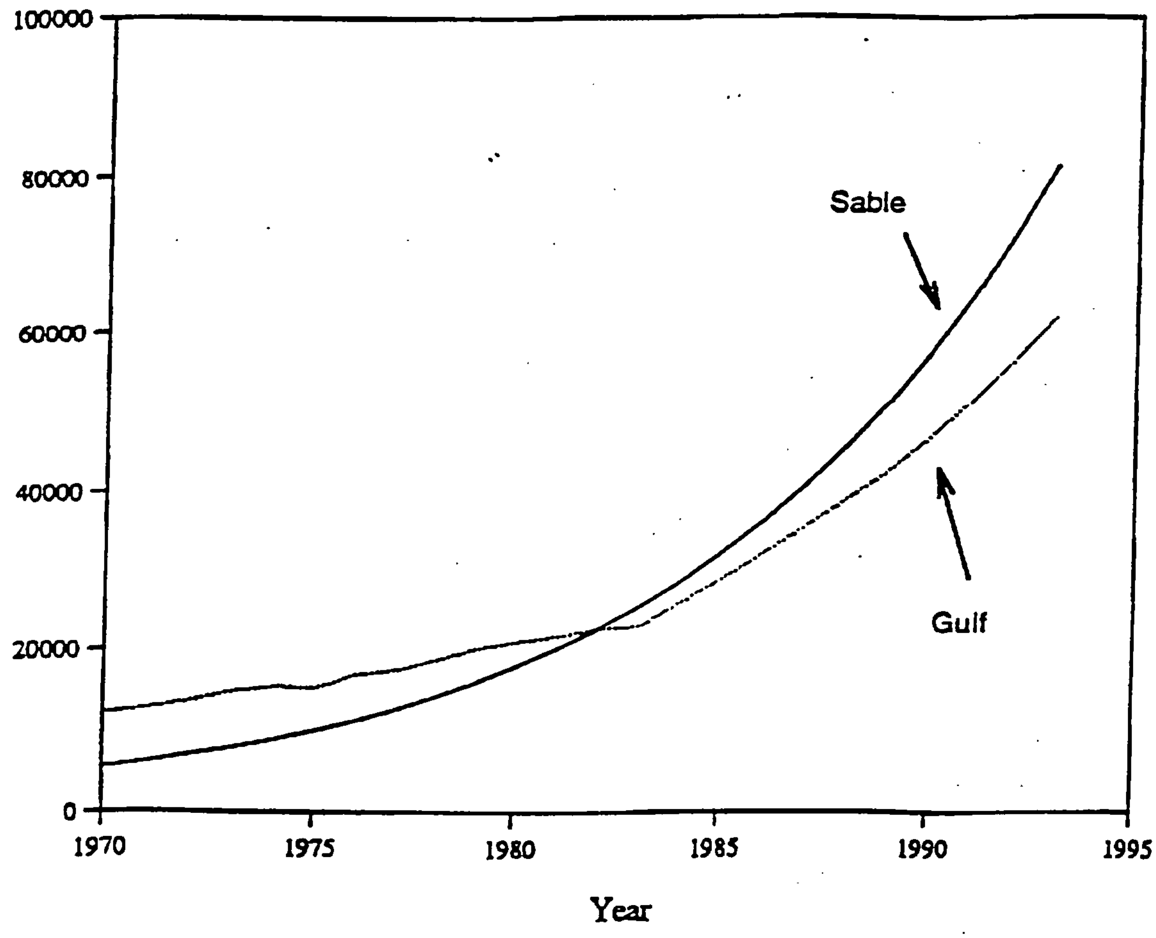
Table 6. Estimated cod consumption by grey seals in eastern Canada using Model 1.

	With Gulf herd distribution 1 (Table 1)					With Gulf herd distribution 2 (Table 1)				
Year	4VsW	NGulf	SGulf	Other	Total	4VsW	NGulf	SGulf	Other	Total
1970	1496	1820	1193	432	4941	1496	2984	840	432	5751
1971	1646	1930	1260	470	5306	1646	3155	887	470	6158
1972	1821	2073	1348	516	5757	1821	3380	950	516	6668
1973	2022	2247	1456	568	6294	2022	3658	1028	568	7276
1974	2231	2386	1538	620	6775	2231	3871	1087	620	7808
1975	2427	2415	1539	661	7041	2427	3890	1090	661	8068
1976	2708	2650	1684	734	7776	2708	4262	1194	734	8898
1977	2984	2779	1751	798	8311	2984	4446	1245	798	9472
1978	3318	3003	1883	880	9084	3318	4790	1340	880	10328
1979	3693	3257	2032	974	9956	3693	5180	1448	974	11295
1980	4092	3465	2145	1068	10770	4092	5484	1532	1068	12176
1981	4523	3640	2231	1166	11560	4523	5726	1597	1166	13012
1982	5007	3837	2328	1276	12449	5007	5999	1671	1276	13954
1983	5529	3983	2383	1390	13285	5529	6175	1717	1390	14811
1984	6210	4460	2666	1560	14896	6210	6912	1921	1560	16602
1985	6962	4953	2954	1745	16614	6962	7665	2130	1745	18502
1986	7809	5516	3284	1955	18565	7809	8528	2369	1955	20661
1987	8755	6124	3637	2187	20702	8755	9453	2625	2187	23020
1988	9810	6784	4017	2444	23056	9810	10454	2902	2444	25611
1989	10985	7486	4417	2729	25617	10985	11511	3194	2729	28419
1990	12306	8276	4867	3048	28496	12306	12700	3522	3048	31576
1991	13785	9148	5361	3406	31700	13785	14010	3884	3406	35085
1992	15443	10111	5904	3805	35264	15443	15453	4281	3805	38982
1993	17300	11172	6499	4250	39222	17300	17036	4717	4250	43304

Table 7. Estimated cod consumption by grey seals in eastern Canada using Model 2.

	With Gulf herd distribution 1 (Table 1)					With Gulf herd distribution 2 (Table 1)				
Year	4VsW	NGulf	SGulf	Other	Total	4VsW	NGulf	SGulf	Other	Total
1970	1473	1793	1155	430	4851	1473	3067	770	430	5740
1971	1622	1911	1223	469	5226	1622	3257	816	469	6164
1972	1794	2053	1308	514	5669	1794	3495	871	514	6675
1973	1991	2224	1412	567	6194	1991	3782	941	567	7280
1974	2199	2369	1496	620	6684	2199	4007	1001	620	7827
1975	2396	2412	1506	663	6977	2396	4041	1014	663	8113
1976	2662	2611	1623	732	7628	2662	4385	1087	732	8866
1977	2939	2758	1702	799	8198	2939	4598	1146	799	9482
1978	3265	2971	1823	881	8940	3265	4944	1226	881	10316
1979	3633	3220	1966	974	9794	3633	5342	1324	974	11274
1980	4027	3428	2077	1069	10601	4027	5653	1405	1069	12153
1981	4453	3609	2165	1170	11396	4453	5909	1470	1170	13001
1982	4923	3783	2246	1279	12230	4923	6157	1528	1279	13887
1983	5442	3949	2313	1397	13101	5442	6358	1584	1397	14781
1984	6097	4374	2556	1561	14589	6097	7064	1743	1561	16465
1985	6835	4853	2833	1747	16268	6835	7824	1935	1747	18341
1986	7665	5396	3148	1956	18165	7665	8686	2153	1956	20460
1987	8593	5990	3489	2189	20261	8593	9617	2392	2189	22791
1988	9629	6632	3851	2447	22559	9629	10622	2645	2447	25342
1989	10787	7338	4245	2735	25104	10787	11721	2919	2735	28162
1990	12085	8125	4682	3057	27949	12085	12953	3222	3057	31318
1991	13543	8992	5162	3417	31114	13543	14307	3555	3417	34822
1992	15171	9941	5686	3819	34617	15171	15784	3919	3819	38693
1993	16997	10985	6260	4267	38510	16997	17399	4320	4267	42985

Figure 1. Total numbers in Sable Island and Gulf of St. Lawrence herds.



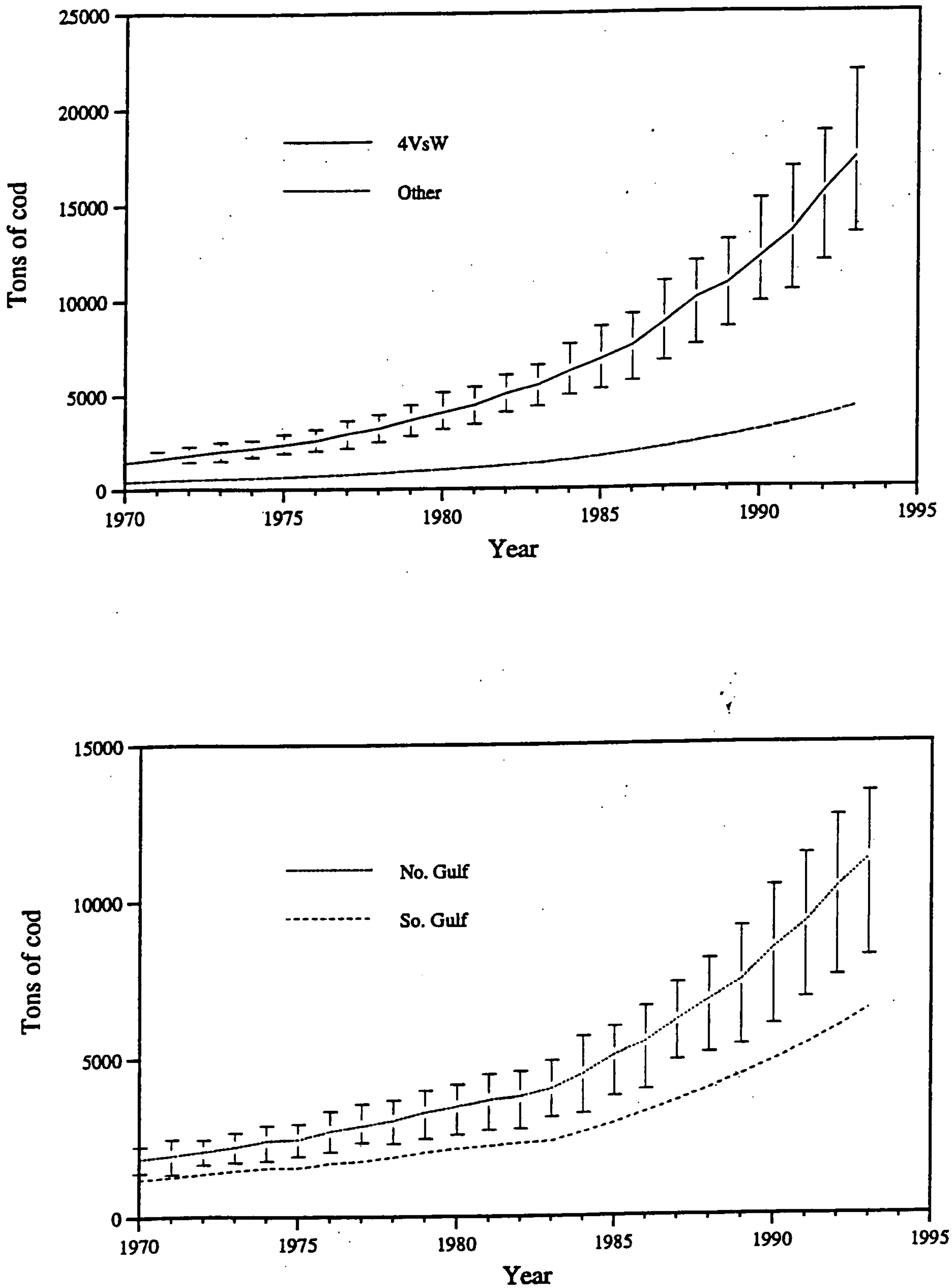


Figure 2. Estimated cod consumption using model 1, and distribution 1. (a) 4VsW with 95% confidence intervals and Other. (b) Northern Gulf with 95% confidence intervals and southern Gulf.

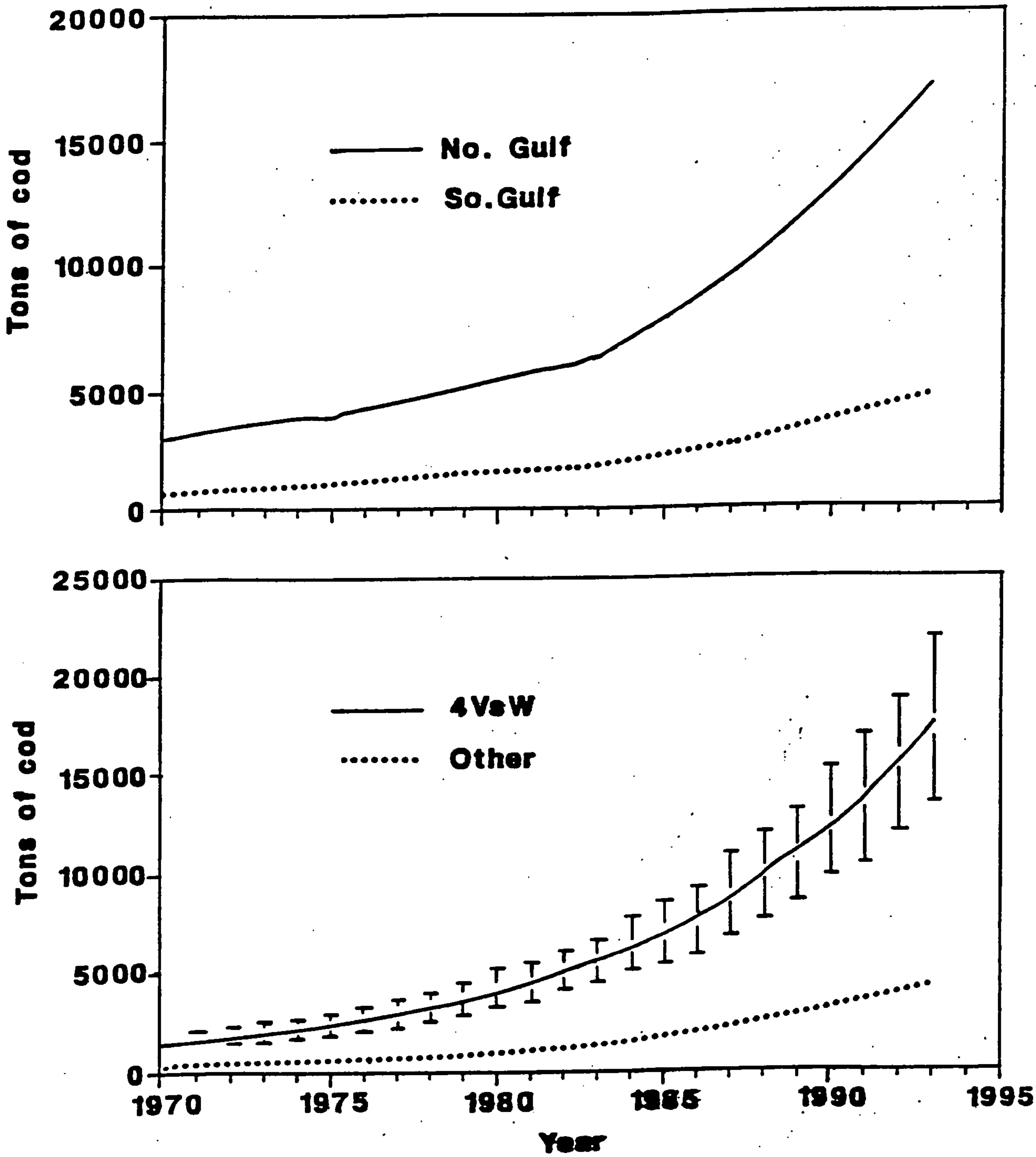


Figure 3. Estimated cod consumption using model 1, and distribution 2, for zones 4VsW and Other (top) and for the northern Gulf and southern Gulf (bottom).

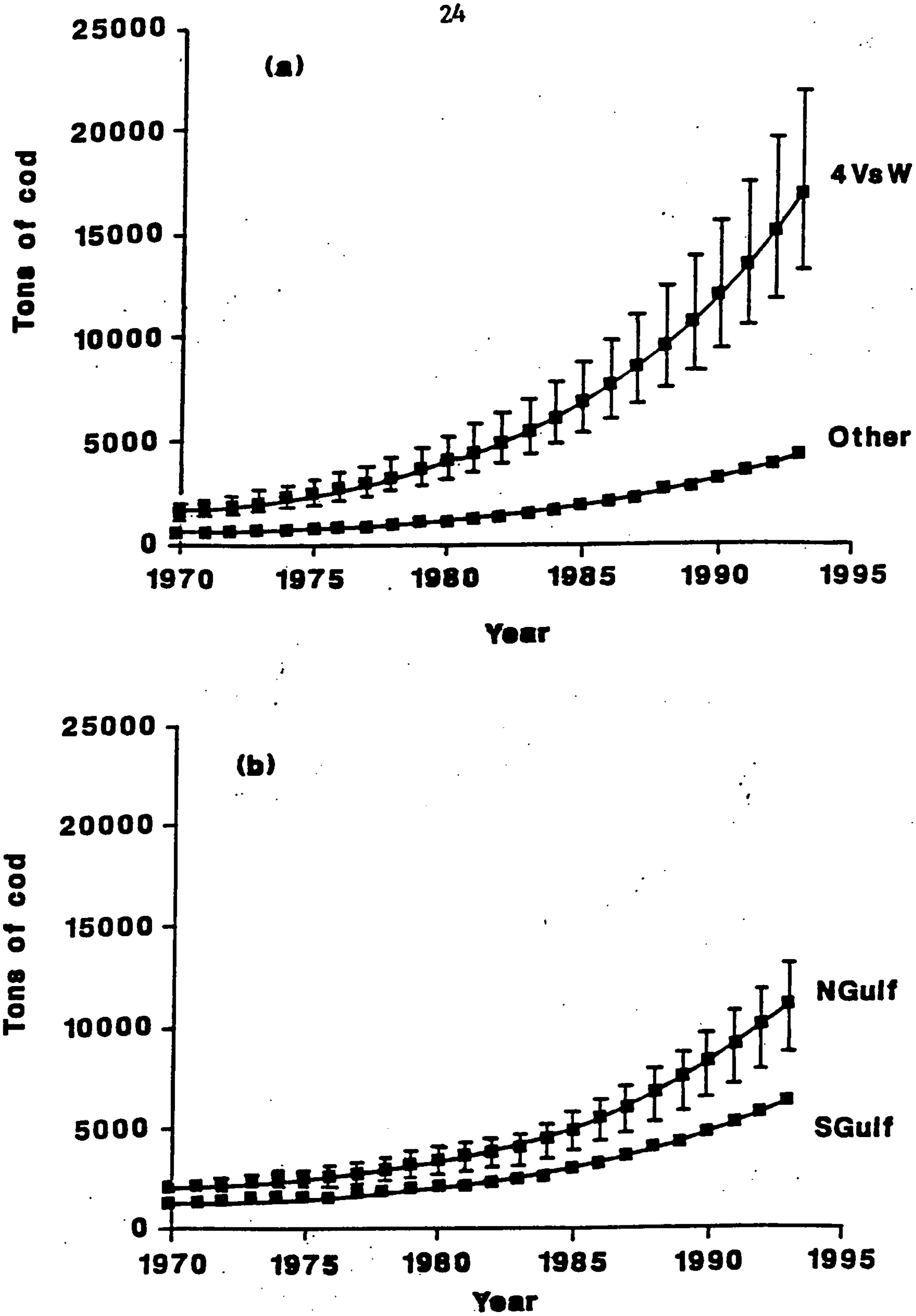


Figure 4. Estimated cod consumption using model 2 and distribution 1. (a) 4VsW with 95% confidence limits and Other. (b) Northern Gulf with 95% confidence limits and southern Gulf.

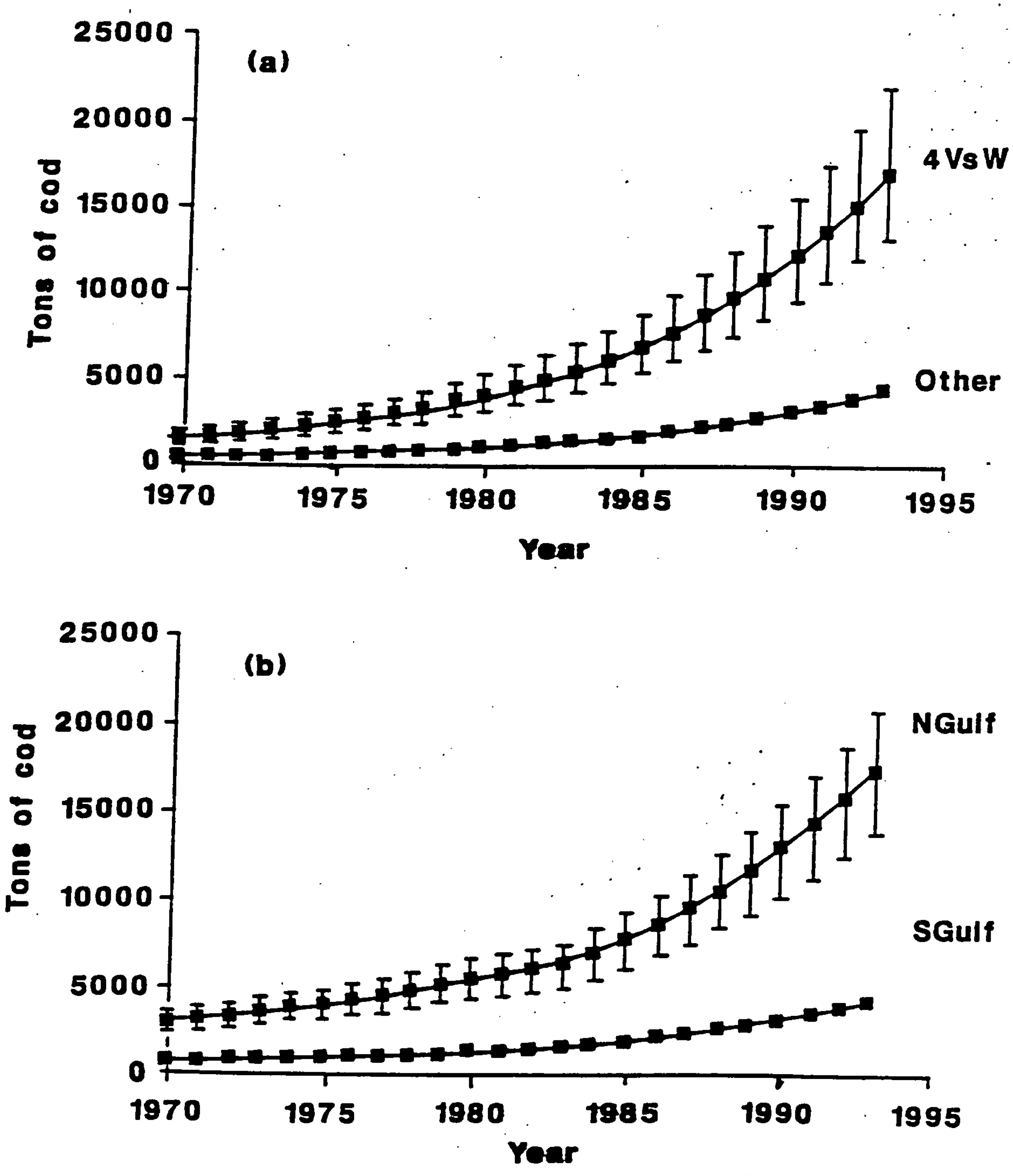


Figure 5. Estimated cod consumption using model 2 and distribution 2. (a) 4VsW with 95% confidence limits and Other. (b) Northern Gulf with 95% confidence limits and southern Gulf.