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A model of grey seal predation on 4VsW cod and its effects on the dynamics and potential yield of cod

by

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Abstract

In 1986, Canada released a three volume royal commission report on seals and sealing in Canada which suggested that grey seals (*Halichoerus grypus*) were responsible for significant financial losses to the fishing industry in eastern Canada . These losses resulted both from predation by grey seals of commercially valuable fish and the link between grey seals and the abundance of the sealworm parasite (*Psuedoterranova decipiens*) in fish of commercial importance. In recent years, a number of studies have been conducted to improve our understanding of the impacts of grey seals on commercial fisheries in eastern Canada.We develop a model to examine trends in the consumption of the 4VsW cod (*Gadus morhua*) stock by grey seals over the period 1970 to 1993. We proceed by developing an age-structured model of the population dynamics of grey seals and the seasonal distribution of grey seals in the 4VsW study area. We estimate the mass-specific energy requirements of seals, the fraction of three size classes of cod in the grey seal diet, and the average energy density of the diet. Annual estimates of grey seal predation mortality on cod are compared with commercial landings and VPA estimates of cod population numbers and biomass at age of 4 VsW cod. Both the Sable Island and Gulf of St. Lawrence grey seal populations increased substantially over the past several decades, such that total population size in eastern Canada in 1993 was estimated at about 143,000 animals. Estimated consumption of prey by grey seals in the 4VsW study area increased from about 11,800 t in 1970 to over 138,000 t in 1993. On average, cod accounted for about 13% of the seal diet by weight. The incorporation of explicit grey seal predation significantly affects the stock-recruitment pattern and yield per recruit of 4VsW cod.

Resume

En 1986, le Canada publiait un rapport en trois volumes dans lequel la Commission royale d'enquête sur le phoque et la chasse au phoque au Canada laissait entendre que le phoque gris (*Halichoerus grypus*) était la cause d'importantes pertes financières dans l'industrie de la pêche de l'est du Canada, pertes imputables à la fois à la prédation de poissons à valeur commerciale par cet animal et au lien entre ce dernier et l'abondance de vers de phoque parasites (*Pseudoterranova decipiens*) chez les poissons d'importance commerciale. Ces dernières années, on a réalisé un certain nombre d'études pour mieux comprendre les effets du phoque gris sur les pêches commerciales de l'est du Canada. Nous élaborons ici un modèle permettant d'examiner les tendances de la consommation de morue de 4VsW (*Gadus morhua*) par le phoque gris de 1970 à 1993, en commençant par modéliser, selon l'âge, la dynamique de la population de phoque gris et la distribution de celui-ci dans la zone 4VsW à l'étude. Nous estimons les besoins énergétiques spécifiques du phoque selon la masse, la fraction de trois classes de taille de morue dans le régime alimentaire du phoque gris et la densité énergétique moyenne de ce régime. Nous comparons les estimations annuelles de la mortalité de la morue due au phoque gris aux débarquements commerciaux et aux estimations d'APV de la morue de 4VsW et de sa biomasse selon l'âge. Tant la population de phoque gris de l'île de Sable que celle du golfe du Saint-Laurent ont augmenté considérablement au cours des quelques dernières décennies, au point qu'en 1993 on estimait à 143 000 animaux la population totale de phoque de l'est du Canada. La consommation estimée de proies par le phoque gris dans la zone à l'étude est passée d'environ 11 800 t en 1970 à plus de 138 000 t en 1993. En moyenne, la morue représentait environ 13 % du poids de la nourriture du phoque. L'incorporation d'une prédation explicite par le phoque gris modifie considérablement la dynamique stock-recrutement et le rendement par recrue dans la population de morue de 4VsW.

Introduction

Seals can be important predators in marine ecosystems (Laws 1977).This has lead to a concern that seals may reduce the yield from commercially valuable fish species (e.g. Beddington, Beverton, and Lavigne 1985, Gulland 1987, Wickens et al. 1992). In 1986, Canada released a three volume royal commission report on seals and sealing which suggested that grey seals (*Halichoerus grypus*) were responsible for significant financial losses to the fishing industry in eastern Canada (Malouf 1986). These losses resulted both from estimated predation by grey seals of commercially valuable fish and the link between grey seals and the abundance of the sealworm parasite (*Psuedoterranova decipiens*) in fish of commercial importance. As a result of recommendations of the commission, a number of studies have been conducted to improve our understanding of the interactions between grey seals and commercial fisheries in eastern Canada. In this paper, we develop a model to examine trends in the consumption of the 4VsW cod (*Gadus morhua*) stock by grey seals over the period 1970 to 1993.

Catches from cod in NAFO subarea 4VsW ranged between 40,000 and 80,000 t from 1958 to 1974 before declining to a low of only 10,000 t in 1977 as a result of reduced stock abundance. Catches increased to 50,000 t as the stock rapidly recovered to a peak in 1985. The abundance of the 4VsW cod population has declined since the mid-1980s, reaching the lowest recorded level in 1993 (Mohn and MacEachern 1994). Over this same time period, the grey seal population in eastern Canada , and particularly that on the Scotian Shelf, has continued to increase and has recently attained the highest level observed since the first estimates were made more than 30 years ago (Mansfield and Beck 1977, Hammill et al. 1992, W. T. Stobo pers comm.).

The major grey seal rookeries in eastern Canada are located in two areas: on Sable Island which is located in NAFO Division 4W and in the southern Gulf of St. Lawrence (Mansfield and Beck 1977). Both juveniles and adults from these major rookeries are known to disperse over large areas of eastern Canada during the non-breeding season (Mansfield and Beck 1977; Stobo, Beck, and Horne 1990). Some mixing of adults is also known to occur during the breeding season, but the degree of mixing is thought to be small (Zwanenburg and Bowen 1990). Although the genetic structure of the population is unknown, for convenience, we consider seals from each of these two areas as representing separate populations.

We proceed by first developing an age-structured model of the population dynamics of grey seals and the seasonal distribution of grey seals with respect to the 4VsW study area. We estimate the mass-specific energy requirements of seals in the population, the fraction of three size classes of cod in the grey seal diet, and the average energy density of the diet. We then compare annual estimates of grey seal predation mortality on cod with commercial landings and virtual population analysis (VPA) estimates of population numbers and biomass at age of 4 VsW cod. Finally, we explore the sensitivity of the model to uncertainty in the parameters and the implications of grey seal predation on yield per recruit calculations and on the stock-recruitment relationship of 4VsW cod under two assumptions about cod natural mortality rate (M).

The grey seal and cod populations are modelled in an interactive Macintosh environment (Black and Mohn 1993). There are three interacting levels of code which give this computer environment its power and versatility. At the lowest level, the bulk of calculations, especially numerically intensive ones, are performed in compiled C. The cod virtual population analysis using a non-linear least squares (NLLS) procedure is an example of this level. The C code is accessed by executing program commands. The user executes commands, or directly manipulates control variables (e.g. assumed selectivity), and writes scripts to control the program in an enhanced version of ExTalk, an embedded language (Betz, 1988). Finally, a Graphical User Interface within which the commands are executed is provided by using the Macintosh Operating System and a commercial interface package (FaceWareTM). The basis for the modelling environment was originally developed for contour analysis and the exploration of geographical data (Black, 1993) and subsequently for fish population assessment (Black & Mohn, 1993).

Seal Population Models

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. In this paper, we have built on the approach used by Zwanenburg and Bowen (1990) by constructing a deterministic, age-structured model similar to a Leslie matrix model. In our model, we assume 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. Reduced male survivorship has been inferred based on the oldest age of males and females observed in shot samples in Canada (Mansfield and Beck 1977) and the United Kingdom (Harwood and Prime 1978) and is consistent with natural mortality patterns observed in other sexually dimorphic pinnipeds (Le Boeuf and Reiter 1988). The above data suggest that few grey seal males survive beyond age 25-30 years, whereas females survive to > 40 years of age. To model these observations, we increased the mortality rate of males age 6 and older by a factor of 3 (Table 1). The resulting mortality patterns for males and females in both population components are shown in Fig. 1. In the model, all seals are assumed to die at 40 years of age.

Pup production estimates from both the Gulf and Sable Island populations were fit using a population projection model with two parameters to scale the underlying patterns. The first parameter scaled the pattern of natural mortality and the second accounted for the estimates of total population size in 1967. The input mortality rates were taken from Zwanenburg & Bowen (1990) with the additional assumption about the mortality rates of males ≥ 6 years of age (Table 1). The population age distributions in 1967 were estimated by iterating the input rates of natural mortality and fecundity until a stable age distribution was achieved. The age-specific estimates of survivorship for males and females in the Gulf and Sable Island components are shown in Fig. 1. These patterns were used as starting values for this study.

The two parameter population model was then optimised with a NLLS fit. Fig. 2 shows the results when fitted to mark-recapture estimates of Gulf pup production in 1984, 1985, 1986, 1989, and 1990 (Hammill et al. 1992). The two estimates for each of these studies were derived from independent samples of the ratio tagged to untagged seals (Hammill et al. 1992). The lower line in Fig. 2 illustrates the effect of DFO culls on the rate of increase in pup production in the Gulf between 1968 and 1984. The resulting trend in Gulf population size is shown in Fig. 3, again reflecting a slow rate of increase until the cull was ended in 1984. The 1993 Gulf population is estimated at 61,900 animals, with a doubling time of about 8 years. The coefficients of variation on the parameter estimates of Gulf pup production were about 40%.

Estimates of grey seals pup production on Sable Island, based on total counts, are available for most years between 1962 and the 1990 (Mansfield and Beck 1977, Stobo and Zwanenburg 1990). However, counts prior to 1976 were often based on short visits to the island and therefore in most cases underestimated pup production (Zwanenburg and Bowen 1990). Thus we have used only pup censuses conducted between 1976 and 1990 (Stobo and Zwanenburg 1990, W. T. Stobo pers. comm) to estimate the trend in Sable Island pup production. The fitted line to the pup census data is shown in Fig. 4 along with estimates prior to 1976 which consistently lie below the line as previously reported. Also shown is a preliminary estimate of Sable Island pup production in 1993, based on an aerial photographic survey (W. T. Stobo pers comm.). Although preliminary, this estimate indicates that pup production on Sable Island continues to increase at about 13% per year. This corresponds to a doubling time of slightly less than 6 years. The 1993 total population is estimated to be 81,600 seals (Fig. 3). The coefficients of variation for the parameters estimates of Sable Island pup production were < 10%.

Fig. 3 also illustrates the geographic shift in the contribution of the Gulf and Sable Island populations to the total number of grey seals in eastern Canada over the 23 year period since 1970. At the beginning of this period, 69% of the total population was of Gulf origin. By 1982 the two populations were about equal in numbers. However, by 1993 only 43% of the estimated total population (about 143,000 seals) was of Gulf origin.

Seasonal Distribution of the Grey Seals in 4VsW

The magnitude of grey seal predation on 4VsW cod depends on the seasonal distribution of both populations. In relation to cod, we assume that seasonal movements are by definition confined to the 4VsW stock area. However, this is not the case for grey seals. The two populations are known to undertake large scale seasonal movements (Mansfield and Beck 1977; Stobo et al. 1990). Our assumptions about the seasonal distribution of grey seals with respect to the study area are given in Table 2. We assumed that adult grey seals that breed on Sable Island are restricted to the 4VsW area during the first quarter of the year. However, it is known that some juvenile seals of Sable origin are found elsewhere at this time of year. To account for this, we have assumed that only 90% of the Sable population were present in 4VsW at this time of the year. Tagging studies show that grey seals from Sable Island subsequently feed throughout Eastern Canada (Stobo et al. 1990). This conclusion is based on mainly coastal mainland tag recoveries with little information on offshore distribution. Because the distribution of tag recoveries cannot be adjusted to account for variation in effort used to recover tags in different areas and at different times of the year, there is considerable uncertainty about the seasonal distribution of the population. Nevertheless, we have used the existing tag recoveries as a rough approximation of the seasonal distribution.

We made the same assumption about the distribution of the Gulf population during the first quarter of the year as used for the Sable population, namely that 90% of the population were in the Gulf, and 10% were elsewhere (i.e., in 4VsW). Less is known about the distribution of the Gulf population at other times of the year, however, tag recoveries do indicate that pups, juveniles, and adults feed on the Scotian Shelf (Lavigueur and Hammill in press, Stobo et al 1990). Again we have used the existing tagging data as a first approximation to the seasonal distribution of the Gulf population in the 4VsW area. In the case of both populations, we have assumed that all age groups show the same seasonal distribution patterns and that these patterns are stable over time.

The Predation Model

Seal energy requirements

Estimates of the average daily metabolic rate (ADMR) of free-living grey seals are not available. In fact, there are few estimates of ADMR of free-living phocid seals in general. Castellini et al. (1992) measured V_{O2} rates in five, free-living, adult Weddell seals while the animals were resting, diving, and during sleep. Resting metabolic rate was 1.6 times greater than that predicted from Klieber's 'mouse to elephant curve' (Klieber 1961) probably because these freely diving seals were feeding and thus food-induced thermogenesis would have raised metabolic rate. Metabolic rate of Weddell seals during short dives was not significantly greater than that during rest. However, metabolic rate during long dives (i.e., 1.4 times Klieber) was significantly lower than the rate of oxygen consumption during short dives. It is clear from this study that diving, whether short or long, is not energetically costly in Weddell seals and that ADMR is about 1.5-2.0 times the predicted standard metabolic rate for animals of similar size (Klieber 1961).

The only grey seal data come from captive studies. Ronald et al. (1984) found that the standard metabolic rate of adult grey seals was about equal to that predicted by the Klieber equation for a mammal of similar body mass. Fedak and Hiby (1984; SMRU report) measured the metabolic requirements of 10 grey seals ranging in age from one month to > 10 yr and in body mass from 43-270 kg. Although these data showed considerable variation at age, Fedak and Hiby (1984) developed the following relationships to estimate average daily metabolic costs of grey seals as a function of age:

for age < 10 yr   ADMR (kcal/kg/d) $= 42.5 - 0.7$ age (yr),
for age ≥ 10 yr   ADMR (kcal/kg/d) $= 35.5$.

Given a metabolic rate of 35.5 kcal/kg/d, an adult grey seal would expend energy at a rate of about twice that predicted by the Klieber equation. Although these data do not include the cost associated with diving, both the above Weddell seal results and recent studies on free-ranging grey seals which demonstrate marked reduction in heart rate during diving (Thompson and Fedak 1993, Fedak and Thompson 1993) suggest that ADMR of adult grey seals is reasonably estimated as two times the Klieber equation.

The mass-specific metabolic requirements of young growing animals are known to be greater than that of adults (Brody 1945, Hart and Irving 1959, Weiser 1984). Based on a review of pinniped data, Lavigne et al. (1986) concluded that the standard metabolic rate of immature, growing pinnipeds was about two times that predicted by Klieber's equation or in other words about twice the adult rate. Worthy (1987) measured standard metabolic rate in neonatal grey seals and found most values lie between 2 and 3 times that predicted by Klieber's equation. Ronald et al. (1984) found that the standard metabolic rate of growing 1-year-old and 2-year-old grey seals was 1.8 and 1.7 times Klieber, respectively. Although there is some uncertainty about the size of the "growth premium" (*GP*) needed to account for the growth of immature grey seals, we have assumed that pups and 1 to 5+ year-old seals require 150%, 140%, 130%, 120%, 110%, and 100% of average daily adult rate, respectively.

We used the following equation to estimate the daily gross energy intake (*GEI*, kcal/d) of an individual grey seal:

$$GEI(a) = GP(a) * (2 * 70 * BM(a)^{0.75}) / (ME - HIF)$$

where a = age 0 to 39 years for males and females, BM = body mass (kg), ME = metabolizable energy (i.e., the proportion of GEI available to the animal), and HIF = proportion of GEI lost to heat increment of feeding, and $70 * BM^{0.75}$ = the Klieber equation. Estimated ME in grey seals fed herring averaged 83 ± 4.8% of gross energy intake (Ronald et al. 1984). Harp seals on a herring diet expended 17% of ingested energy on HIF (Gallivan and Ronald 1981). Given the absence of data in grey seals, we have used this value.

The body masses of male and female grey seals as a function of age were determined from shot samples collected in the Gulf of St. Lawrence between 1988 and 1992 (M. Hammill unpublished data). These data were fit using NLLS to a Gompertz equation of the form:

$$W = p_1 * \exp(p_2 * (1 - \exp(- p_3 * a))$$

where W is the body mass (kg) and *a* is age (yr) from 0 to 39. The growth curves for males and females and estimates of the Gompertz parameters and their CV's are shown in Fig. 5 and Table 3, respectively. Predicted body mass at age from the Gompertz model were used in all subsequent calculations.

Prey size and composition of grey seal diets

The fraction of the population energy requirements accounted for by cod was determined from recent studies on the composition of grey seal diets. Estimates of the percent wet weight of different prey in the diet of grey seals were derived from otoliths and other hard parts recovered in 198 grey seal stomachs containing food from inshore sites along the Eastern Shore of Nova Scotia and 393 faecal samples collected on Sable Island during the period 1988-1993 (Bowen, Lawson, and Beck 1993; Bowen and Harrison in press; Bowen and Harrison unpubl.). Cod comprised from 1.6% to 44.1% by weight of the diet in the above studies (Fig. 6). Although the estimates varied considerably, there was no evidence of a trend in the percentage of cod in the diet over time. Variation in the species composition and energy content of grey seal diets is shown in Table 4. The average energy density of the diet in these 13 samples varied from 1.2 to 2.1 kcal/g wet weight.

The above estimates of diet composition are based largely on the identification of otoliths and squid beaks recovered from grey seal stomachs or faeces. Thus, prey without hard parts that are resistant to digestion may be underestimated in the diet by this method. This will tend to systematically overestimate the importance in the diet of species that have robust otoliths, such as cod and other groundfish. Although we have no way of knowing how serious this bias may be in the case of grey seals, we have assumed that 20% of the diet by weight may not have been seen and therefore we have adjusted the average energy of the samples listed in Table 4 accordingly. We assumed that this 20% correction for unseen prey had a caloric value of 0.8 kcal/g which would be appropriate for many invertebrates.

The relationship between otolith length and body length of cod and other prey were used to estimate the size of prey consumed by grey seals (Bowen et al. 1993, Bowen and Harrison in press). Based on the combined sample of measured cod otoliths and average weight-at-age (Mohn and MacEachern 1994), we estimated that cod <30 cm, from 31-45 cm, and >45 cm fork length accounted for 44%, 36%, and 20% by weight of the cod in the diet, respectively. These length classes are roughly equivalent to 0-2 year-old cod, 3 to about 50% of 4 year-old cod, and 4+ year-old cod, respectively (Mohn and MacEachern 1994). In the model, we assume that the percentage of cod eaten by length class is constant over time.

Food consumption of the grey seal population

Given our lack of knowledge on the functional form of prey selectivity by grey seals, we have used a demand model which assumes that there is sufficient prey (i.e., cod) to satisfy the demand of the predator and so the percentage cod in the diet remains constant irrespective of the relative abundance of cod. This is in contrast to Lotka -Volterra and other models in which the prey abundance affects the amount consumed. Daily *GEI* of the population was calculated for each sex by multiplying numbers of grey seals at age by the appropriate *GEI(a)* and then summing over ages. The *GEI* was converted from daily weight of food eaten into a quarterly energy requirement in tons by dividing the requirement by the average energy density of the prey (see Table 4) and scaling this up by the number of days per quarter. Grey seal predation by sex was estimated for each quarter and size class of cod. The proportion of each population in 4VsW by quarter were taken from Table 2. Both the quarterly total biomass of prey and percent of cod in the diet were calculated. Each of the size classes of cod in the diet were converted from tons to numbers of individual cod using an average weight of 0.2, 0.8 and 1.4 kg for the fish ≤30 cm, 31-45 cm, and > 45 cm, respectively (Mohn and MacEachern 1994).

Mean total annual food intake by grey seals in the 4VsW area increased from an estimated 12,000 t in 1970 (rounded to the nearest 1000 t) to about 138,000 t in 1993. The uncertainty in these estimates is considered below in the section on the sensitivity of the model. Our assumption that 20% of the diet was unseen affected both the percentage cod in the diet and the total energy intake. The percentage of cod in the diet decreased by 25% while the average energy density of the diet decreased by about 8% resulting in an increase in quarterly energy intake of about 9%. For a 4 year old male, this would mean that the estimated quarterly food intake increased to 0.59 t after the correction for unseen prey from 0.54 t before the correction. Approximately 13% of the adjusted food intake was cod. Total food intake was increased by about 8% by adjusting the diet for unseen prey which was assumed to have a relatively low energy density.

The biomass and numbers of cod reported in commercial landings and those estimated to have been consumed by grey seals using the base-run parameters of the model are shown in Fig. 7 and 8. For the most part, cod taken by the commercial fishery are larger fish than those taken by grey seals (Bowen et al. 1993, Bowen and Harrison in press), therefore the two curves in these figures can be viewed as representing separate fleets with relatively little overlap in size selectivity. The estimated mean biomass of cod consumed by grey seals increased from about 1,500 t to 17,300 t over the period 1970-1993 (Fig. 7). The commercial landings over this same period showed a roughly bimodal distribution with landings declining from about 60,000 t in 1970 to 10,000 t in 1977, then rising to a peak of nearly 60,000 t in 1986 before declining to a record low of only 3,474 t in 1993 (Fig. 7). The same overall patterns are seen when both landings and grey seal predation on cod are expressed in terms of numbers of fish (Fig. 8). However, in the case of landings, the fishery took almost twice as many fish during the early peak than during the later one, reflecting the fact that small cod accounted for a much greater fraction of the landings during the early 1970's. The 1993 consumption by grey seals is estimated at about 48 million cod, comprising mostly fish <30 cm in length.

Sensitivity of the predation model

Our estimates of grey seal predation mortality on cod depend on the precision of data used in the model and the validity of our assumptions where data are currently unavailable. We have used two approaches to assess the sensitivity of model estimates to uncertainty in input parameters: bootstrapping and varying the magnitude of input parameters. The effects of uncertainties in the average energy content of the seal diet and the fraction of the diet that is cod was assessed by bootstrapping (Fig. 9). Bootstrapping (Efron, 1982) is a computer intensive technique in which the underlying data (See Table 4) are resampled, the analysis repeated and the results compiled. We have 13 estimates of the average energy in seal diet which is used to convert daily caloric requirements into a daily ration. Our bootstrapping procedure resampled with replacement the 13 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. Shown in Fig. 9 are the 95% error limits in cod consumption when both average energy and the percentage of cod in the diet were simultaneously bootstrapped. The mean consumption when both parameters are resampled tended to be greater than the base run because of a slight negative correlation between average energy density and percent age of cod in the diet.

The sensitivity of model parameters was examined by independently changing parameters used in the predation model by 10% (Table 5). A base run is made using the values of the various parameters as listed above for the year 1990. Then one of the parameters, for example the seal weight at age, is increased by 10% over all ages of males and females. The model is run again and the cod and total prey mass consumed are then compared to the base run and the difference expressed as a percent of the base run. A sensitivity of 10% would mean that food consumption by grey seals is directly proportional to a change in that parameter.

As expected, the estimated cod consumption by grey seals in the 4VsW area is quite sensitive to the size of the Sable Island population, the fraction of *GEI* available to the animal, the percent of cod in the diet, the energy density of the diet, the Klieber multiplier, and the body mass of seals. Given our assumptions about the quarterly distribution, within the study area, the model results are relatively insensitive to a change in the size of the Gulf population. Both cod and total food consumption are insensitive to a 10% change in the correction factor of 20% for prey that may not be detected by the methods used to determine diet composition. Although we have changed each parameter independently in order to isolate their effects, in reality they will often covary, for example changes in the percent cod and the average energy density of the diet.

A final type of sensitivity to be investigated is the sensitivity to the assumptions used in the consumption model to extrapolate the amount of cod in the diet outside of the data region for stomach contents, 1989 - 1992. As mentioned above, we have chosen a constant percentage model tin which an average 12.6% of the seals total consumption by weight is cod. For comparison, a second model is chosen in which the amount of cod eaten is proportional to the biomass of cod in the 3 size groups.

$$E_S = q_S \ B_S \ N$$

where E_S is tons of the cod eaten, B_S is the estimated 4VsW cod biomass, q_S is a scaling coefficient , N the number of seals and s is a subscript denoting the size class of the cod. By finding the average cod biomass, amount eaten, and number of seals in 4VsW over the 4 year period 1989-1992, the average q_S may be solved for. These qs are then held constant for the entire simulation period and the amount of cod consumed in each quarter is calculated and accumulated into annual totals. In the following discussion we call this model the proportional percentage model. This model essentially assumes that all other food items compensate over the period of investigation such that when the cod biomass doubles, its relative abundance to other prey items also doubles. This assumption is required because data are not currently available to estimate the abundance of many of the other known prey items.

When the diet is bootstrapped to estimate variance in cod consumption in the demand model, the individual amounts of cod are saved and used to produce a pool of qs for estimating variances in the proportional percentage model. This is done by averaging E_S for the 1989-1992 for each of the bootstrap runs. The qs are then sampled with replacement to derive bootstrap estimates for the proportional percentage model. 100 replicates were used to produce the qs. Then, 100 replicates of the 24 year period for the proportional percentage model are produced by drawing a q for each year.

There are of course many other models of predator-prey interaction (See for example Beverton, 1985) that could be chosen which may involve prey selection, saturation and other considerations. Because of the lack of relevant data, we have not explored them.

Effects of Seal Predation on Cod

Once the predation by seals has been estimated in terms of numbers of cod, it is possible to investigate the potential impacts of this predation on the 4VsW cod stock. The effect of the commercial fishery on the 4VsW cod population is assessed annually (Mohn & MacEachern, 1994) using virtual population analysis (VPA). The data cover the years 1970 - 1993 and ages 1-15 years. Catch at age and survey at age data are fit to a population model using an NLLS similar to the methods used above to estimate the seal population size (Mohn and MacEachern, 1994). The catch at age is converted into numbers of cod at age subject to assumptions about M. Therefore, the natural mortality of cod, which is only poorly known, is a key parameter of the cod VPA model. By convention, it is assumed that the M of 4VsW cod is 0.2 for all ages. This assumption has little impact in the context of the population assessment of cod because it is a "virtual" population and is used to estimate allowable catches. The effect of this assumed M is removed when the virtual population is converted into projected catch. However, when we wish to estimate seal predation mortality rate, the consumption by seals is in absolute biomass or numbers of cod as opposed to the virtual values in the VPA. In this context, assumptions about the magnitude and age-specific pattern of M become quite significant.

There have been few attempts to measure age-specific M in cod. Some authors (Beverton & Holt, 1959, Pauly, 1980) have inferred M from other biological characteristics such as life span and growth rate. An ICES working group has investigated this problem for groundfish in the North Sea for over a decade. Anon. (1993) reported M's of 0.8, 0.35 and 0.25 for ages 1-3 and 0.2 for age 4 and older for North Sea cod. Because 4VsW cod grow much slower than North Sea cod (for example, an age 3 North Sea cod at 2.6 kg weighs more than a 9 year old cod from 4VsW), we have assumed that juvenile M of 4VsW cod is higher and persists at high levels for 1 year longer than reported for North Sea cod. We have used the following vector of M's, denoted MR: 1.0, 0.8, 0.6, 0.4 for ages 1 to 4, respectively and 0.2 for the ages 5-15. To assess the difference between these two assumptions about M on estimates of seal predation mortality, we have run all analyses twice; once with M = 0.2 across all ages and again using the vector MR.

Grey seal predation mortality on the three size classes of cod were estimated by first doing a standard VPA using the commercial catch at age as input and then performing the NLLS as described in Mohn & MacEachern (1994) which results in population estimates and fishing mortalities. The consumption of cod by seals was then added to the commercial catch and the VPA was repeated. In this way, the seals were treated as an additional fishing fleet. This process was iterated once to ensure that the patterns observed were stable (for details on tuning VPA's see Mohn & Cook, 1993). This combined mortality was then partitioned into deaths from the commercial fishery and those due to grey seals.

If the seal predation mortality were simply added to either the standard value of M = 0.2 or MR, the recruitment at age 1 and population sizes would be increased because the total M would be larger. It is unlikely that seal predation is completely additive, some compensation among the components of M undoubtedly occurs. However, at present we do not know how much compensation might occur. Therefore, both to allow comparisons with the standard VPA results and to reflect our uncertainty about the interaction of components of natural mortality, M was reduced so that the average recruitment of cod from 1970 - 1974 was the same (i.e., within 1%) with and without seal predation. This meant reducing M to 85% of 0.2 and reducing M to 97% of MR before adding in the seal predation component of natural mortality, M_S.

Seal predation mortality

Fig. 10 shows the annual mortality rate caused by seals for the three size classes of cod defined above. When M = 0.2 was assumed, the smallest size class of cod consistently had the highest mortality rates, increasing rapidly in the early 1980's to about 0.33 by 1990-1991, but then falling rapidly to 0.15 as the 1990 year-class grew beyond this size class (Fig. 10a). The rate of seal predation mortality on larger cod was generally <0.05 until the late 1980s when mortality rose quickly as the stock declined. When the vector MR was assumed, the estimated mortality rate caused by grey seals dropped considerably on the smaller size classes of cod, and did not begin to increase until the mid to late 1980's (Fig. 10b). This result was expected, since predation by seals was now being compared with a higher residual natural mortality which implied a larger cod population in the VPA. Nevertheless, even in this case, total mortality due to seals M_S was > 0.2 by the late 1980s. Seal predation mortality on larger cod was largely unaffected by our assumptions about M (Figure 10 a,b).

The mortality attributable to seal predation may be put into context by comparing it with both fishing and total mortality (Fig. 11). In this analysis, mortality due to seals (Seal Predation in the Figure) and due to the fleet (F - Seals of F - No Seals in the Figure) were averaged over ages 2-8. The reduction in total mortality (Z - Seals in the Figure) seen in the late 1970's was due to the nearly total exclusion of foreign fishing effort in 4VsW with the extension of jurisdiction to 200 miles. Under either assumption about background M, the contribution by seals (Seal Predation in the Figure) to total mortality, Z, was small until the late 1980's, but became more pronounced in the 1990s as the number of grey seals continued to increase while the cod population decreased. Interestingly, seal predation mortality on the 2-8 year old cod leveled off in 1993, despite a continued increase in the number of grey seals, reflecting the presence of the relatively strong 1990 year-class.

The pattern of recruitment of age 1 cod from 1970 to 1991 with and without explicit grey seal predation in the model is shown in Fig. 12. Because VPA' s cannot estimate the youngest ages in the most recent years, the series was truncated at 1991. For both assumptions about M, the first few years in the series correspond well because of the normalization of background M to match the average recruitment for 1970-74 mentioned above. In the absence of explicit seal predation, recruitment declined rapidly during the 1980s (Fig. 12a). However, when seal predation is explicitly included in the model, recruitment at age 1 appeared not to have been so severely reduced (Fig. 12a). Under the assumption of MR similar patterns emerge, but the effect of grey seal predation was reduced and the magnitude of the number of recruits was about 6 times greater due to the higher total mortality (Fig. 12b).

Stock-recruitment

The addition of explicit seal mortality to the model also affects the stock-recruitment pattern of 4VsW cod (Fig. 13). In this figure, the estimated number of age 1 cod recruits is plotted against the approximate spawning stock biomass of the previous year and thus the numbers on Fig. 13 represent year-classes. For each year, there is a number which shows the location of the parent stock and corresponding recruitment in the absence of explicit seal predation. This number is joined by a line to a dot which is the same year's position after including predation by grey seals. In interpreting Fig. 13, it is important to remember that the underlying assumption in the model is that seal predation is additive. If there is strong compensation in the components of M, then the effect of predation on recruitment would be less (i.e., the length of the lines shown in these figures would be shorter). The lines are too short to be visible for the early years, but under both assumptions about M the lines increase in length over time (Fig. 13a,b). Without explicit seal predation, recruitment fell significantly through the 1980's despite a high biomass of spawners and continued to fall at moderate spawning stock size in the late 1980's. Adjusting for the effects of grey seal predation substantially increased the initial size of the 1983-1990 year-classes. In fact, the 1990 year-class is estimated as one of the strongest observed. If M = 0.2 was assumed, recruitment seems to have remained reasonably strong during the 1980s, but only a small fraction of these young fish survived to commercial size. This effect was less pronounced if MR was assumed (Fig. 13b). However, in neither does case seal predation account for the decrease in year-class size during much of the 1980s compared to that observed during the 1970s, suggesting an increase in other types of natural mortality perhaps associated with environmental changes.

Yield per Recruit

A yield per recruit analysis was carried out to assess the potential impact of grey seal predation on the yield of 4VsW cod. Fig. 14 compares the effects of average predation mortalities for the 70s, 80s and the period 1990-93 to results based on the two assumptions about M in terms of yield per recruit. The yield per recruit model balances cod growth with removals and deaths at age. The plots show that yield per recruit of cod may have been reduced by >50% as a result of seal predation in the most recent period, provided that M_S is additive. As in the case for the recruitment analysis, the magnitude of the yield varies by about a factor of about 7 under the two assumptions about M.

These yield per recruit comparisons must be interpreted with caution because the relative importance of different sources of natural mortality on cod cannot be quantified. The grey seal component has been explicitly estimated, but it is not known how other sources of natural mortality might respond to a change in the number of seals. However, it is likely that there would be some level of compensation in that if one predator is reduced, the mortality caused by other predators may respond to the increase in food availability. The dotted curves in Fig. 14 are based on the assumption that grey seal predation mortality is essentially additive (i.e., no compensation). If, on the other hand, there was complete compensation for the increase in seal predation by a reduction in other sources of M, then grey seal predation will have had no effect on yield per recruit. Clearly, neither of these extremes is likely and thus the effect of grey seals on yield per recruit of cod will probably fall between the dotted curves and the solid curve in Fig. 14.

The implications of the yield per recruit must be made in the context of the effects explicit seal mortality has on recruitment levels. There is a degree of compensation between the reduction in the yield per recruit and the augmentation in the level of recruitment. The following table shows the various estimates of the strength of the 1990 year-class under the 4 scenarios under consideration. For example, under M = 0.2 mortality schedule, the estimate of the 1990 year-class doubles when seals are included while the yield per recruit is less than half with seals. The net effect is about 27% loss in potential yield from this year-class. The potential yield from the 1990 year-class is the product of the yield per recruit and the year-class size. Implicit in this calculation is that fishing, predation and natural mortality patterns remain constant over the duration of this year-class in the fishery, or up to about the year 2000. A similar impact is seen under M = MR.

Model	No Seals	Seals	No Seals	Seals
Natural mortality	0.2	0.2	MR	MR
Recruits (1990 YC Millions)	55	105	390	520
F0.1	0.17	0.27	.17	0.29
1990s Yield per recruit at F0.1 (g)	400	156	54	29
Potential yield from 1990 YC (kt)	22	16	21	15

Potential effect of grey seals on projected cod recruitment

To assess the probable impact of seal predation on cod recruitment, we bootstrapped recruitment estimates projected from the VPA. The recruitment series with M = 0.2 and explicit seal predation from 1970 to 1990 were placed in a pool for resampling. An exponential weighting function was applied to the recruitment estimates so that recent levels were more probable then early ones. The time constant chosen was 0.1 which meant that the most recent recruitment was about 7 times more probable than the 1970 value. This form of projection was chosen because of the lack of a strong stock-recruit relationship but a reduction in recruitment levels in recent years. Fig. 15 shows the recruitment series (solid line) and the same series minus the removals by seals in the smallest, cod size class in our model (dashed line) for the period 1970-1990. 250 bootstrap replicates were drawn for each of the three years, 1993-1995. The means and standard deviations for the projections are shown as solid lines. To estimate the removals by seals in the smallest, cod size class, the grey seal population was projected using the parameters described in Table 1.

To estimate the uncertainty about these population projections, we used the results of recent British work. Hiby et al. (1992) conducted an analysis of the error distribution of the size of the North Rona component of the British grey seal population based on estimated pup production; a method quite similar to that used in this study. They reported that the errors were asymmetric and that the 95% limits were 65% and 172% of the mean. We used a beta function to produce a distribution with the desired asymmetry. Because of the similarity of the underlying data, we assumed the range of the error for the Sable population was the same as in the British study. To account for the lower precision of the Gulf pup production data, the 95% range was expanded to 35 and 200% of the mean. Two hundred replicates of the seal population sizes for 1993-1995 with the beta error distribution were produced and the cod consumption estimated under both assumptions about M. The numbers of cod in the smallest size class were subtracted from the 250 replicate 3-year cod recruit series (Fig. 15, dotted curve). The effect of seal predation on projected cod recruitment differed rather dramatically under the two assumption about M. When MR is used, there is no discernible difference in the projected recruitment with or without seal predation. However, if M = 0.2 is used, the model predicts that few recruits would survive in the presence of seal predation.

Two models (constant vs proportional percentage cod) were assumed to extrapolate the percentage of cod in the years for which diet information was not available. Prior to the mid 1980s, the results are quite dependent on which of the two is chosen (Figure 16). The constant percentage curve is a smoothly increasing trend which reflects the increased abundance of seals in 4VsW since 1970. The 95% confidence limits are estimated from 250 bootstrap replicates of the 13 diet samples. The proportional percent cod model shows a peak in the early 80s when cod abundance was high. This peak is about 3 times the cod consumption of the constant percent model which means that cod would have been about 40% of the diet as opposed to the 12.6% used in the constant percent model. 40% is well above the highest percentage seen in our data (Table 4) and probably is an unrealistic high value for a quarterly average. From about 1986 to 1993 the error ranges of the two models overlap.

Discussion

Based on the results of this analysis, predation by grey seals prior to the mid 1980's was unlikely to have been a important source of mortality on 4VsW cod compared to other sources of natural mortality. However by 1993, grey seal consumption of cod is estimated at about 17,300 t (approximate confidence limits from 13,000-22,000 t) compared to the 3,474 t landed by the commercial fishery. Most of this grey seal predation was on cod ages 1-4 (i.e., pre-recruits to the fishery).

Our estimates of grey seal predation on 4VsW cod are sensitive to uncertainties in the underlying data, to parameter estimates derived from these data or assumed on the basis of theory, and to uncertainties in the structural form of the model. We have attempted to incorporate some of the sources of uncertainty in our results, but considerable further work needs to be done with respect to the confidence limits about our estimates. 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. Thus, the model results are extrapolations of the past and not of the present.

Validity of model assumptions

There are two kinds of assumption inherent in our analysis: those concerning parameters of the model and those concerning the structure of the model. First, we discuss assumptions with respect to the parameters of the model.

i. Food Consumption

We begin with the dynamics of the two grey seal populations. We have assumed that the age-specific pregnancy schedule of both populations was constant over the period 1970 to 1993. Although, age-specific pregnancy rates will have varied to some extent, recent unpublished data collected in the Gulf of St. Lawrence (Hammill pers. comm.) do not suggest that fecundity has changed since the studies by Mansfield and Beck (1977). We have also assumed that age-specific mortality rates of grey seals have remained constant for the Sable Island population. Again, while this cannot be strictly true, the exponential increase in pup production on Sable Island suggests that population parameters have been reasonably constant over the period of the simulation. In the case of the Gulf population, the mortality schedule has clearly varied over time as a result of the cull on the breeding grounds between 1967 and 1984. We have explicitly included the effect of these culls in the dynamics of the Gulf population.

Overall, we are reasonably confident of the dynamics of these two populations over the past several decades, although evidence for trends in the Gulf population size is much less convincing than that for Sable Island. However, neither population can continue to increase exponentially indefinitely. At some point, density-dependent changes in population parameters will alter current population trajectories. We have not considered density dependence in the model, to date, as the empirical evidence suggests that such factors have not affected the dynamics of the these populations in eastern Canada.

Our estimates of the size and species composition of grey seal diets are based on the identification of prey from recovered hard parts in stomach contents and faeces collected between the fall of 1988 and winter of 1993 (Bowen et al. 1993; Bowen and Harrison in press, unpubl data.). The potential biases associated with these methods have been discussed by a number of authors (eg. Jobling and Breiby 1986; Harvey 1989). Despite potential sources of error, estimates of the percent weight of prey in the diet from recovered hard parts represent the state of the art in this area. Nevertheless, it is important to bear in mind the potential for bias when interpreting the results of the model.

There are no quantitative data on grey seal diets on the Scotian Shelf prior to 1988. Thus in the model , we have assumed that the composition of grey seal diets is either constant at the mean level or is sampled from the values observed between 1988 and 1993 (see Table 4). Although estimates of percent by weight are not available, we do have frequency of occurrence data from eastern Canada for earlier periods (Table 6). These data clearly indicate that cod was frequently consumed by grey seals during the period 1970 to the present. Frequency of occurrence data is known to underestimate the importance of cod in the diet grey seals relative percent wet weight (Benoit and Bowen 1990a, Bowen et al. 1993). Thus the data in Table 6 suggest that cod may have represented a larger fraction of the grey seal diet in the past. Even if this were the case, the trend in the estimate consumption of cod by grey seals would be largely unaffected. Recent data appears to represent the range of variation of cod in the diet of grey seals over the period used in the model.

Based on estimated fish lengths from recovered otoliths, we distributed grey seal predation across three size classes of cod. We have assumed that the proportion of each size class is constant in the model, however, these proportions will undoubtedly vary. Several studies have found that predation by pinnipeds is positively related to year-class size of the prey (Bailey and Ainley 1982, Sinclair et al. 1994). Therefore, we might expect grey seal predation to respond to variation in year-class size of 4VsW cod and other prey. However, given the lack of variation in cod year-classes in the 1980s coupled with the lack of annual estimates of the percent by weight of cod in the diet, we are not able to include this possibility in the model at present.

We have made a number of simplifying assumptions in calculating the energy requirements of the two grey seal populations. In particular, we have not explicitly accounted for seasonal variation in energy requirements associated with the cost of reproduction and moult. This approach was taken for several reasons. First, the construction of detailed individual energy budgets requires the estimation of a large number of parameters, each measured with error. Second, for some of the parameters, such as percent of time swimming, little information exists. Therefore the inclusion of detail in many cases results in a loss of precision in the model. Third, although reproduction is costly, much of this expense is cancelled by the reduced energy requirements during the moult (Ryg and Oritsland 1991). Also, when expressed in terms of energy requirements of the population, the error in not explicitly modelling the cost of reproduction is about 5% (Olesiuk 1993). Finally, field measurements indicate that an allometric equation can be used to reasonably estimate the ADMR of free-ranging phocid seals. There is uncertainty about the growth premium needed to account for the higher metabolic requirements of juveniles, but as it affects only the first few age classes it will not have a large impact on overall consumption.

Consumption of cod by grey seals is largely a function of effective population size, that is, the total population times the proportion of the population feeding on cod. To approximate the seasonal movements of this highly mobile and wide-spread species, we have modelled predation quarterly. However, the quarterly distribution of the two populations is quite uncertain and this uncertainty translates directly into uncertainty in the effective population size and thus the consumption of cod and other prey. We have used the geographic distribution of existing tag recovery data to gain a rough idea of what might be reasonable. This is an area where current research promises to significantly improve the present situation. Satellite tags and geolocation time-depth recorders have been deployed on several dozen adult grey seals over the past two years (M. Hammill pers. comm.; W. D. Bowen unpubl.). Within several years, we could be in a position to use these data to improve estimates of seasonal distribution of grey seals.

ii. Predation Mortality

To estimate the mortality rate of cod implied by the consumption of cod by grey seals, we used the estimated numbers-at-age of cod from a VPA under two assumptions about M. Our estimates of predation mortality are averages, they do not reflect the uncertainties in either the numbers-at-age of cod in the population or the estimates of the numbers eaten by grey seals. This work remains to be completed.

The natural mortality rate on young cod from sources other than seals, has a significant effect on the estimated cod mortality by seal predation. However, under either of the assumptions about M in the present study, by the late 1980s M_S alone is greater than 0.2 , the rate usually used in population assessments of this cod stock. Our results also indicate that M_S has probably increased significantly over the past 8 years.

The impact of seal predation mortality on the dynamics of cod depends heavily on the extent to which this mortality is additive or is compensated for by a decrease in other sources of natural mortality. The number of recruits is sensitive to the background level of M and to the presence or absence of seals. By comparing recruitment series under various model scenarios to the spring and summer groundfish survey cod abundance indices it may be possible to discriminate which of them best fit these data. Such a validation exercise should consider both local and large scale distributions of cod.

Related to the question of compensation of natural mortality is the question of what are the other sources of natural mortality on 4VsW cod. In other marine ecosystems, fish predators appear to be the major source of M (Overholtz, Murawski, and Foster 1991; Bax 1991; Livingston 1993), particularly on young of the year fish. On the eastern Scotian Shelf, only limited data are available on fish predators of cod (Kohler and Fitzgerald 1969).

Seal predation mortality is a function of predator biomass, food "preferences" of seals, and the quantity of food available. In the present model, we have assumed that there is sufficient cod available to satisfy the demand of seals, independent of both the number of seals and the biomass of cod. We have constructed the model in this way, not because we believe that it is a good representation of the way grey seal predation works, but because we have little empirical data to support another approach. However, by analogy with other vertebrate predators, there are theoretical reasons for preferring other models. A number of studies of vertebrate predator-prey systems suggest that grey seals may exhibit a type III functional response (Holling 1965), whereby predation mortality increases from zero to a maximum and then slowly declines as prey abundance continues to increase. The functional response of seal predation to changes in the abundance of cod and other seal prey will play an important role in determining the impact of seals on cod dynamics. However, given the mobility of grey seals, we might also expect a numerical response of grey seals to changes in prey abundance throughout their distribution. The combined effect of grey seal predation responses to prey abundance need to be evaluated. Continued monitoring of grey seal diets on Sable Island, coupled with estimates of prey abundance from research surveys, could provide an insight into the dynamics of grey seal predation on cod.

The projected cod recruitment in Figure15, with and without seal predation, assumes that the grey seal population will continue to increase at its estimated current rate and that recent levels of recruitment are most likely to occur in the near future. These assumptions may be reasonable. It may be less reasonable to assume that cod will continue to make up the same fraction of the grey seal diet that it has in the past, although recent data were collected during this period of low cod biomass. In any case, it is clear that there is great uncertainty about future cod recruitment, with or without grey seal predation included. If M on young fish is as high as we have assumed under MR then the model predicts that seal predation will not have much impact on the level of recruitment observed. However, if M = 0.2 then, the model predicts that seal predation may negatively affect cod recruitment. Although they cannot be viewed as extreme cases, the two assumptions about M should provide reasonable bounds on the effect of grey seal predation on cod recruitment using this simple demand model.

iii. Structure of model

We chose a demand model for the functional form of the interaction between seal and cod for the analysis of potential impacts of seals on cod; that is that on average seals will find a certain amount of cod irrespective of its relative abundance. The amount was 12.6% of the diet by weight. 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 decreases to very low levels while seal herds increase. A second choice of functional form was chosen for comparison of the amount of cod consumed but was not used in subsequent analysis. The second form assumed that the amount of cod consumed per seal would be proportional to the cod biomass in each of the three cod size categories. The peak to trough ratio for the cod biomass is about a factor of 4 from 1970 - 1993 and represents a large 'signal' which is superimposed on the even larger change in seal numbers. The overlap in error bars in recent years suggests that the two models are indistinguishable. The non-overlap in earlier years shows that the assumption about the functional form of the fraction of cod in the diet has a greater effect than the variation in the diet samples. The large changes in both predator and prey over the period of investigation may be sufficiently large to allow the determination which of the two models is more likely. We have only looked at two models for the interaction between seals and cod. Beverton (1985) discusses a number of alternative models for the functional response to a change in prey abundance.which might be considered in future work.

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. We have also not included other species in this model. Cod are not major prey items for fish in this or adjacent areas (Kohler & Fitsgerald, 1969, Langton & Bowman 1980) and details of predation by birds are not known, but it is unlikely that they would remove many cod after age 1. So again because of the absence of data to support a more complex model, one was not developed.

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Table 1. Population parameters used to model the Sable Island and Gulf of St. Lawrence grey seal populations. Preg = proportion pregnant

	Weight		Sable Preg	Sable Natural mortality		Gulf Preg	Gulf Natural mortality	
Age	Male	Female		Male	Female		Male	Female
0	52	48	0.00	0.249	0.249	0.00	0.339	0.339
1	71	63	0.00	0.043	0.043	0.00	0.059	0.059
2	92	78	0.00	0.043	0.043	0.00	0.059	0.059
3	113	92	0.00	0.043	0.043	0.00	0.059	0.059
4	133	106	0.16	0.043	0.043	0.16	0.059	0.059
5	151	118	0.71	0.043	0.043	0.71	0.059	0.059
6	168	129	0.91	0.125	0.043	0.85	0.179	0.059
7	184	138	0.91	0.125	0.043	0.85	0.179	0.059
8	197	147	0.91	0.125	0.043	0.85	0.179	0.059
9	208	153	0.91	0.125	0.043	0.85	0.179	0.059
10	217	159	0.91	0.125	0.043	0.85	0.179	0.059
15	246	175	0.91	0.125	0.043	0.85	0.179	0.059
20	256	181	0.91	0.125	0.043	0.85	0.179	0.059
25	259	183	0.91	0.125	0.043	0.85	0.179	0.059
30	261	183	0.91	0.125	0.043	0.85	0.179	0.059
35	261	184	0.91	0.125	0.043	0.85	0.179	0.059
39	261	184	0.91	0.125	0.043	0.85	0.179	0.059

Table 2. Proportion of each population of grey seals within the 4VsW area by quarter of the year. First quarter beginning January 1.

	Quarter of the year			
Population	1st	2nd	3rd	4th
Sable	0.9	0.5	0.5	0.8
Gulf	0.1	0.2	0.2	0.1

Table 3. Parameter estimates and coefficients of variation (CV,%) of the Gompertz fits to body masses of male and female grey seals.

	p_1	CV %	p_2	CV %	p_3	CV%
Male	51.958	5.5	1.615	3.2	0.217	6.7
Female	47.796	4.4	1.346	3.1	0.223	5.5

Table 4. Estimates of % wet weight and energy density of grey seal diets from scats and stomach contents collected on the Scotian Shelf, 1988-1993.

	Sample													Energy	
Species	1	2	3	4	5	6	7	8	9	10	11	12	13	(kcal/g wet wt)	Source
Cod	17.6	6.1	13.9	20.1	33.5	19.2	44.1	12.7	3.5	4.1	1.6	17.2	3.7	1	Bowen unpubl
Herring	65.8		9		33.2									2.6	Murie and Lavigne 1992
Pollock	7	6.8												1.2	Jensen 1979
Mackerel	0.4		47.4		9.9									2.4	Bowen et al 1993
S. hake	3.2	25.8	0.7	0.6	2.5	5	3.1	1.5	0.4	0.2	0.1	5.6		1	Bowen unpubl
Squid	1.4	26.6	12.9	4.2										1	Bowen et al 1993
Sand lance		32.7		75.1		56	49.4	75.1	78.7	76.1	77.8	67.2	85.3	1.6	Birkhead & Nettleship 1987
Flatfish					14.6	18.5	2.9	7.8	10.7	15.7	19.4	7.5	7.9	1	Bowen unpubl
Redfish						1.2		0.4	2.7	2.4	0.7	1.5	0.4	1	Lawson unpubl
Haddock					2.6									1.3	Murie & Lavigne 1992
Total	95.4	98	83.9	100	96.3	99.9	99.5	97.5	96	98.5	99.6	99	97.3		
Ave energy	2.1	1.2	2.0	1.5	1.7	1.3	1.3	1.5	1.5	1.5	1.5	1.4	1.5		
Source	a	a	a	a	b	c	c	c	c	c	c	c	c		

a = Bowen et al. 1993, b = W. D. Bowen unpubl., c = Bowen and Harrison in press

Table 5. Percentage change in cod and total annual consumption of prey in response to a 10% increase in input parameters.

Parameter	Base Value	Cod	Total Prey
Sable population sizw	57467	8.5	8.5
Gulf population size	46781	1.5	1.5
% Sable pop. in 4VsW, 2nd quarter	50	1.6	1.6
% Gulf pop. in 4VsW, 2nd quarter	20	0.5	0.5
Correction for unseen prey	0.20	- 0.9	0.7
Metabolizable energy (ME)	0.83	- 11.2	- 11.2
Heat increment of feeding (HIF)	0.17	2.6	2.6
% wet weight of cod in diet	12.6	10.0	0.0
Average energy density of diet (kcal/g)	1.42	- 8.3	- 8.3
Klieber multiplier	2	10.0	10.0
Seal weight at age	from Table 1	7.4	7.4

Table 6. Estimates of percent relative frequency of occurrence of cod in grey seal diets between 1969 and 1987.

Years	Location	% Relative frequency occurrence of cod	Source
1969 - 1971	Atlantic Canada	16.9	Mansfield and Beck 1977
1963 - 1987	Nova Scotia	13.6	Benoit and Bowen 1990a
1983 - 1984	Sable Island	21.3	Benoit and Bowen 1990a

Figure 1. Stable survivorship patterns for Sable and Gulf grey seal populations

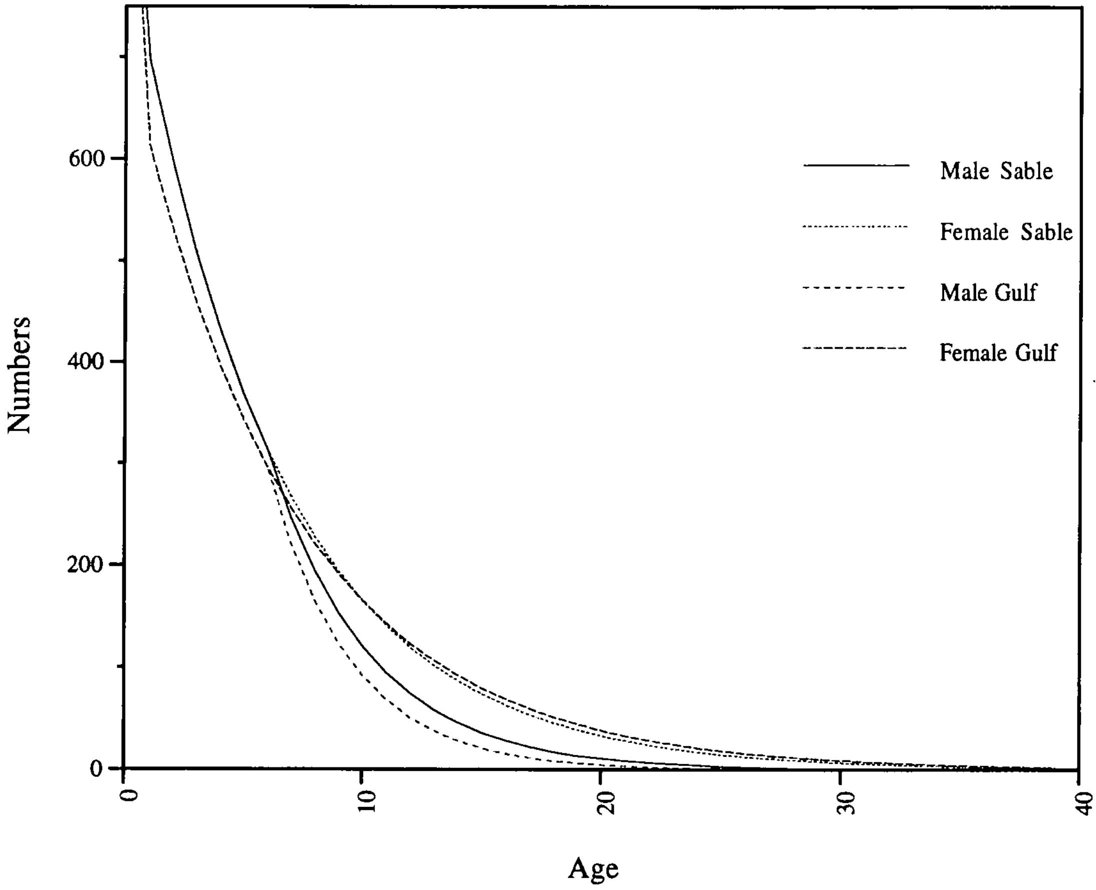


Figure 2. Population model and data for Gulf of St. Lawrence grey seal herd. Hatching shows size of cull.

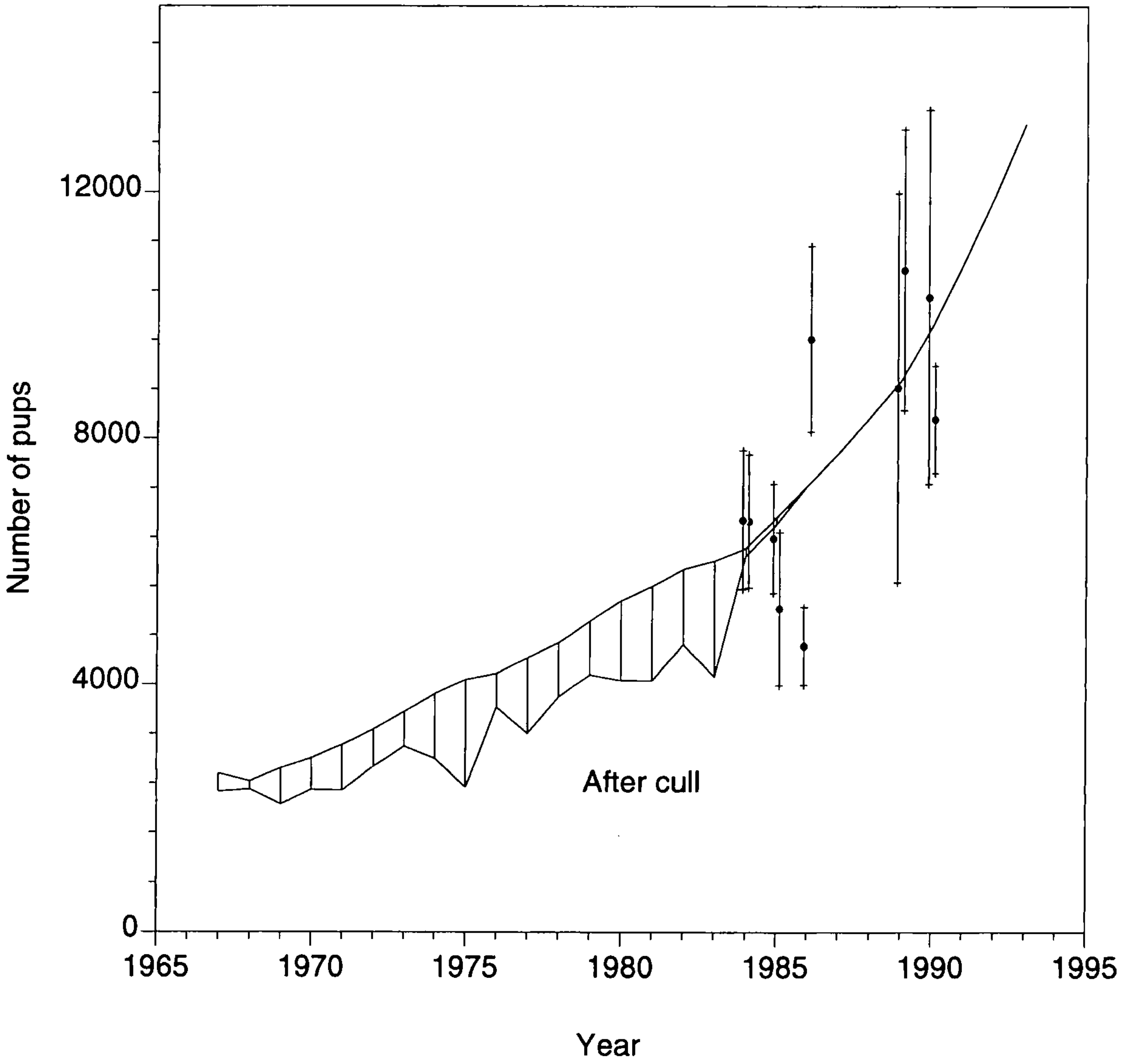


Figure 3. Total numbers of grey seals in Sable Island and Gulf of St. Lawrence herds.

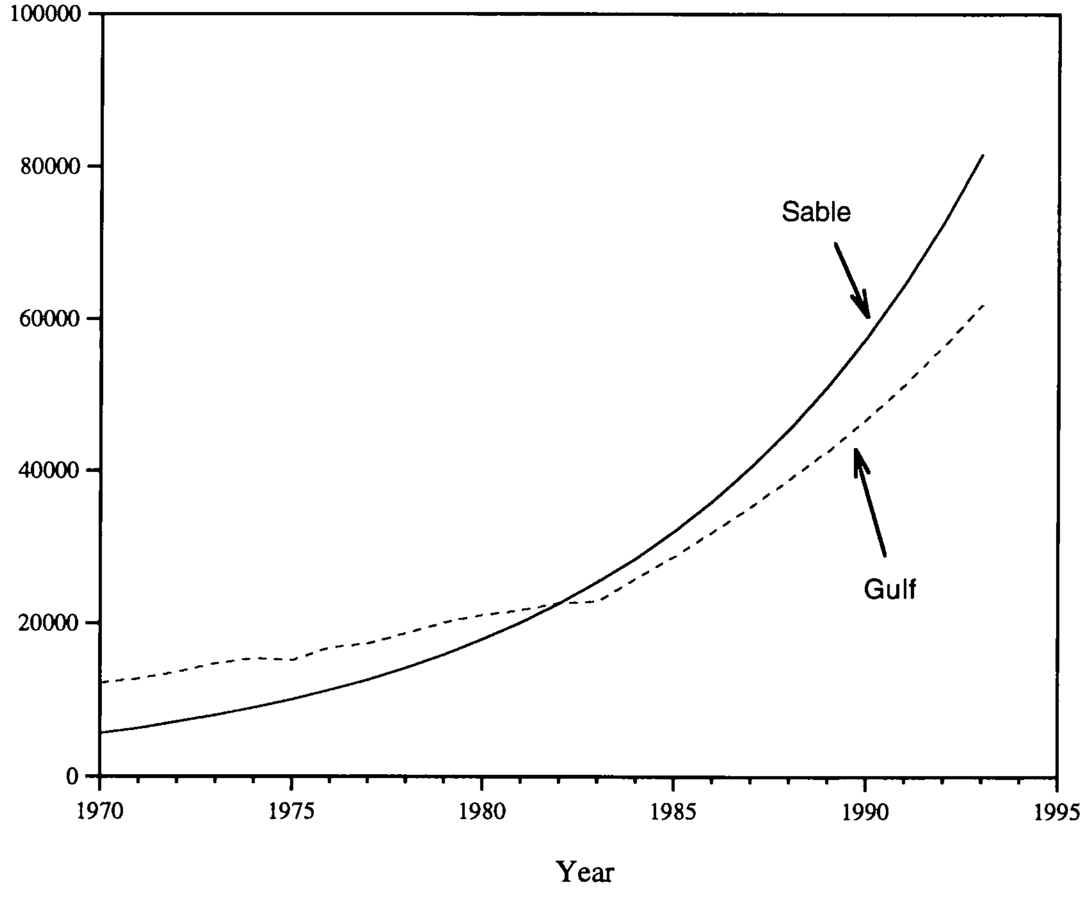


Figure 4. Population model and data for Sable Island grey seal herd.

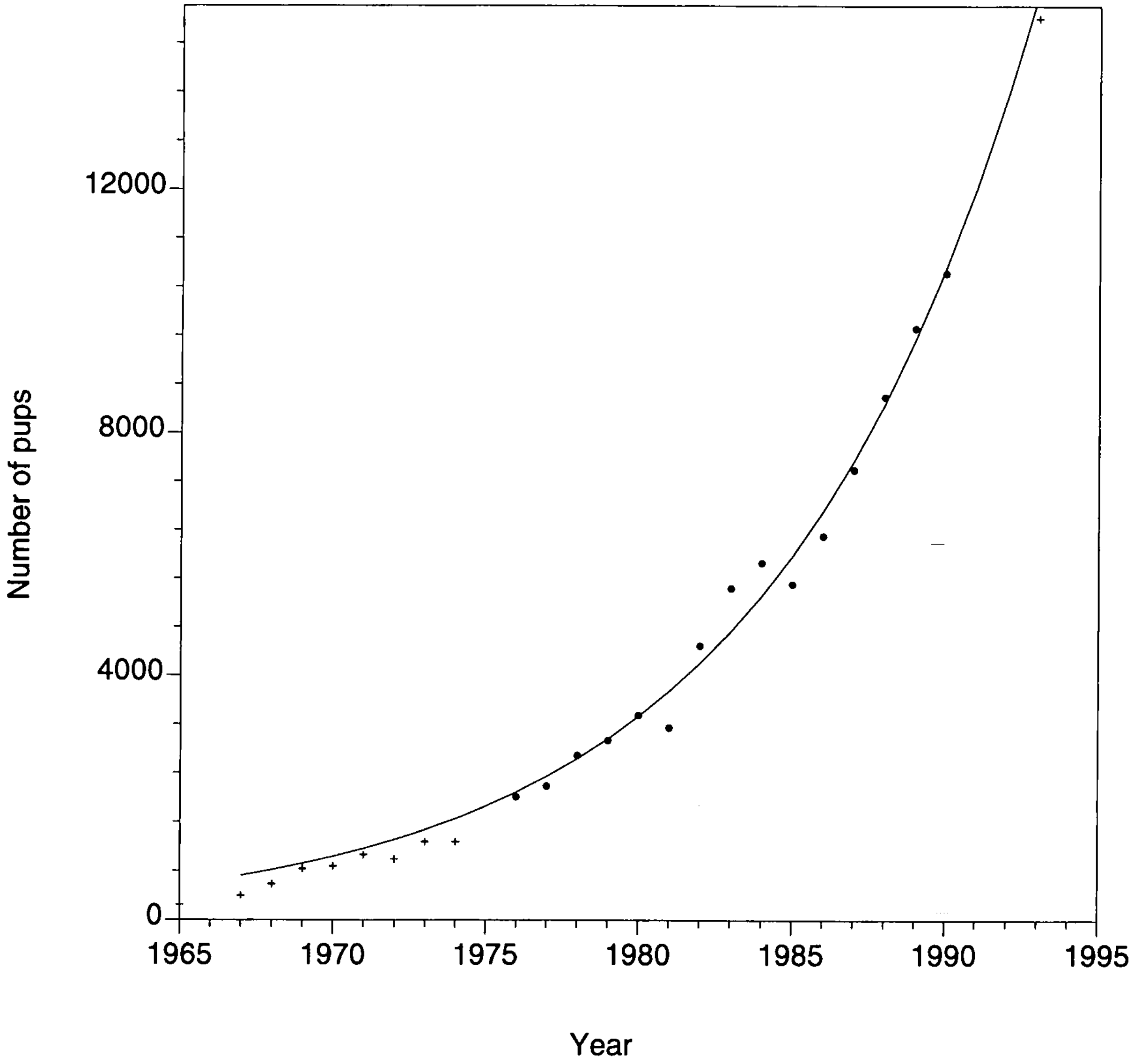


Figure 5. Gompertz growth models fit to male and female grey seal data.

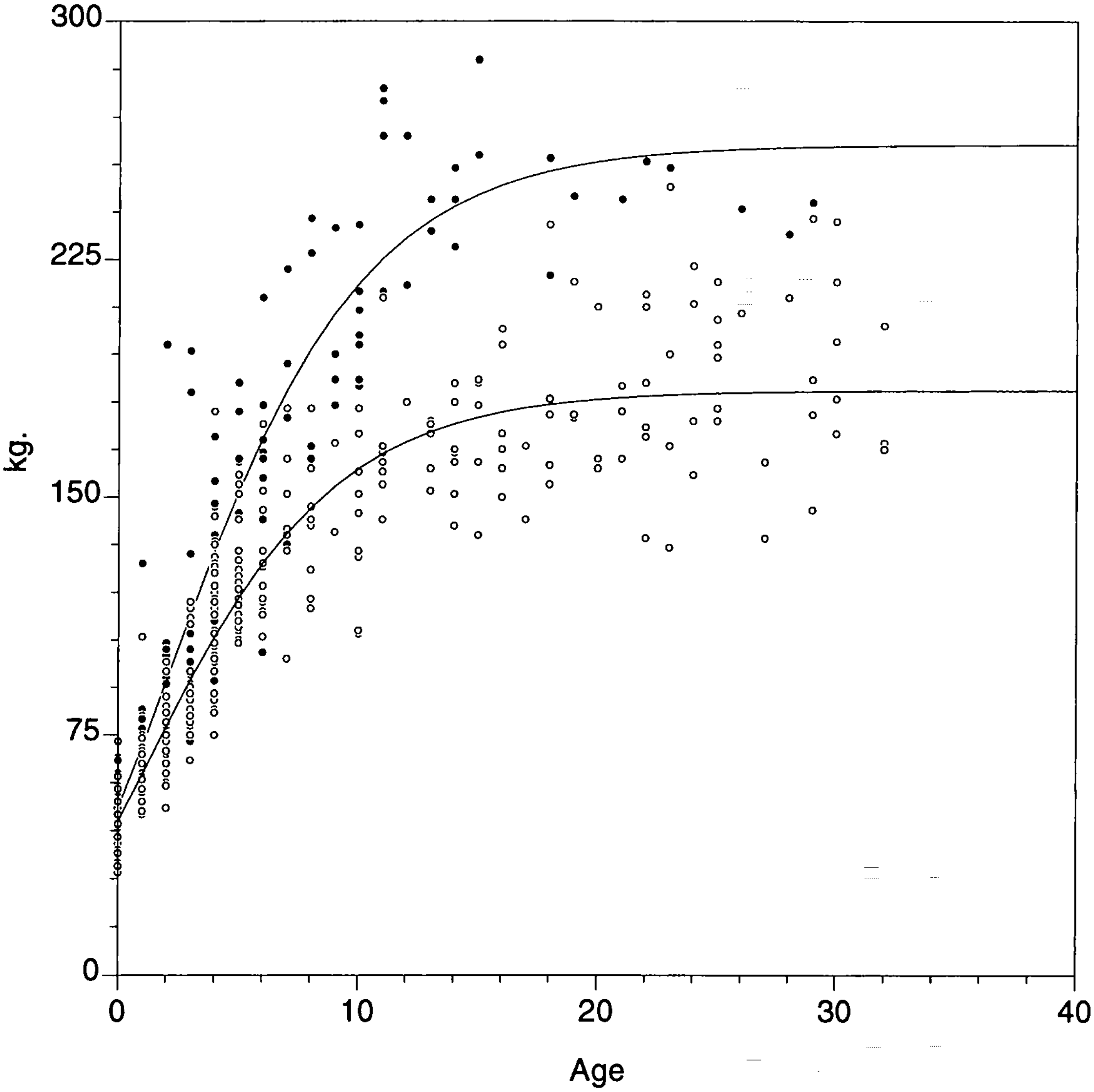


Figure 6. Percent cod by weight in grey seal diets

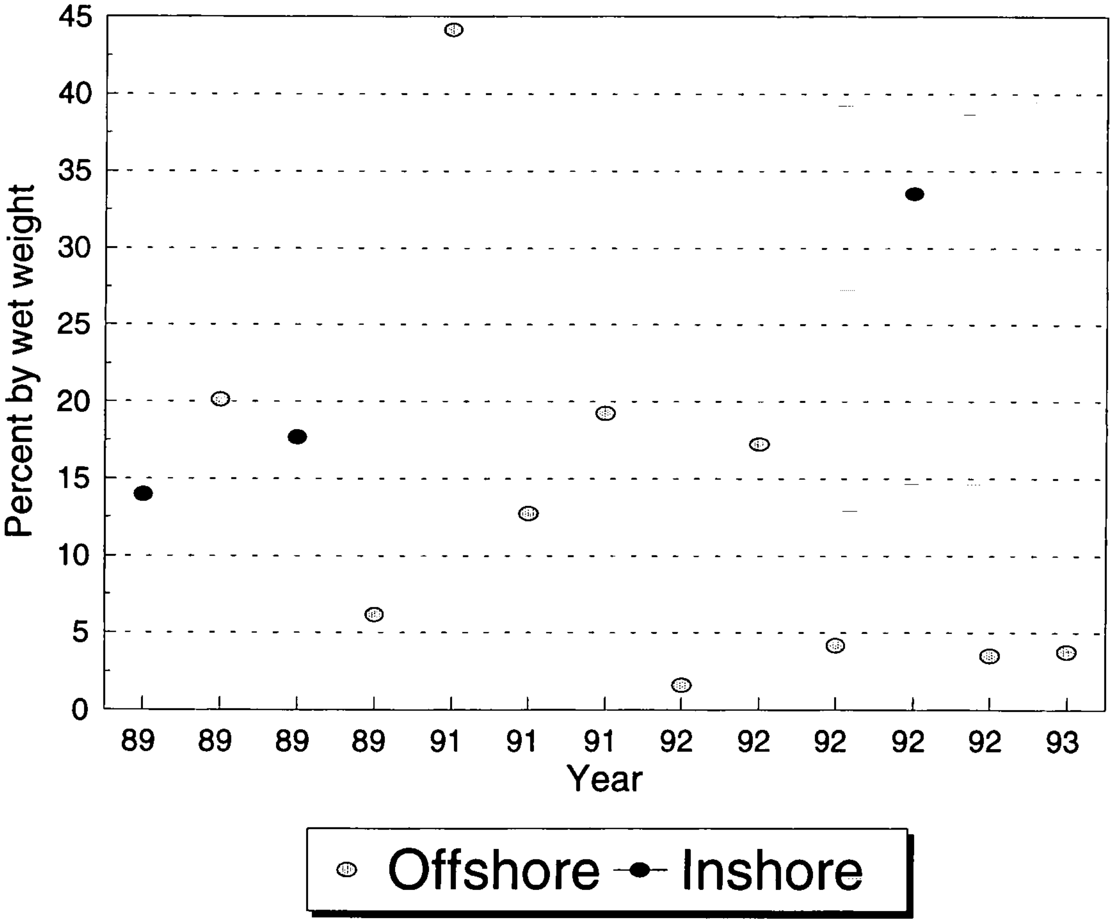


Figure 7. Landings of 4VsW cod and estimated mean seal consumption in tons of fish.

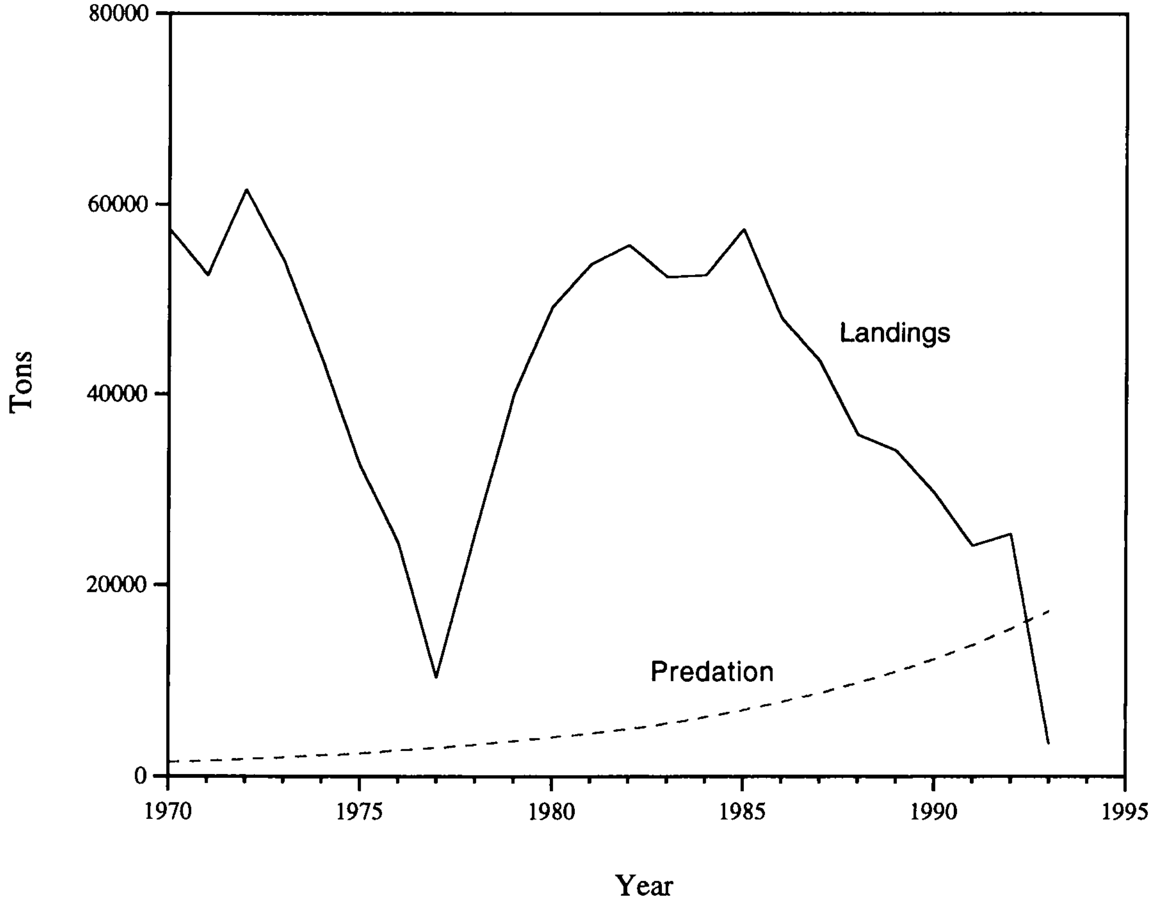


Figure 8. Landings of 4VsW cod and estimated mean seal consumption in numbers of fish.

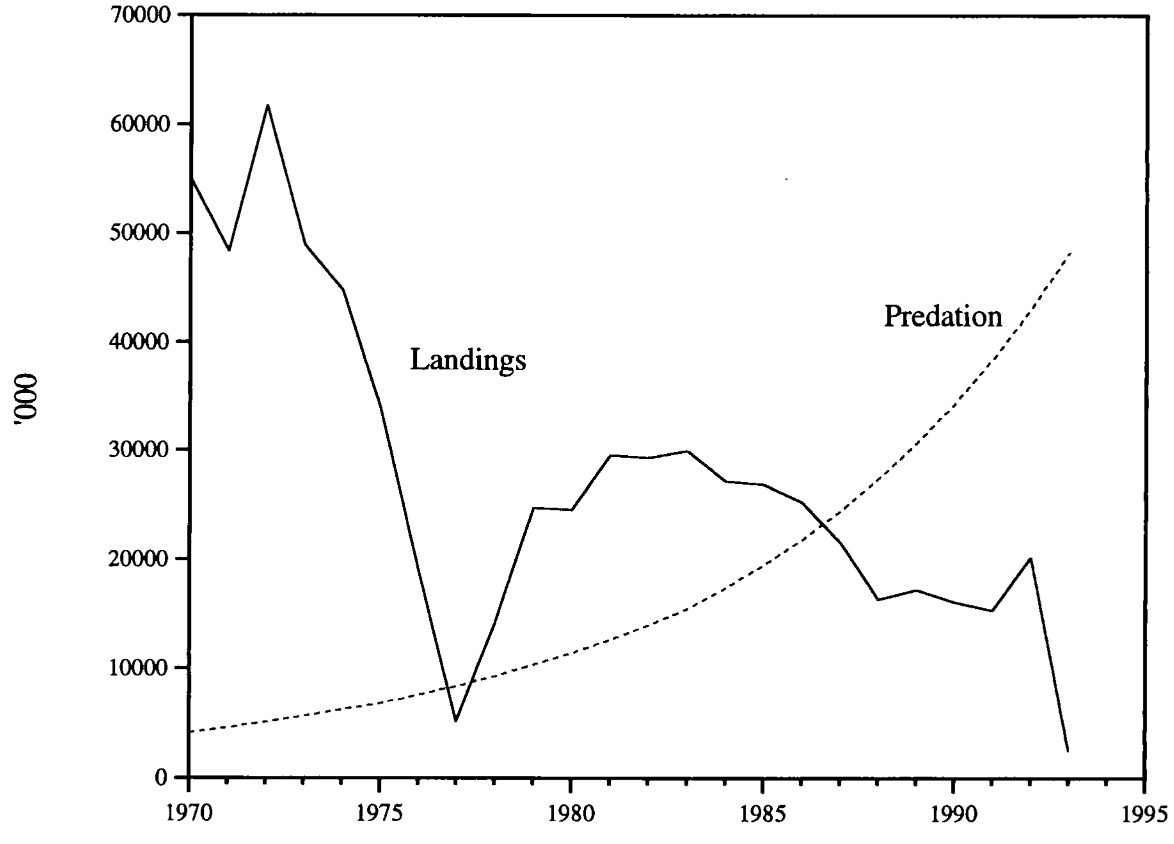


Figure 9. Total cod consumption (mt) by grey seals with 50 and 95% error bars estimated by bootstrapping diet data

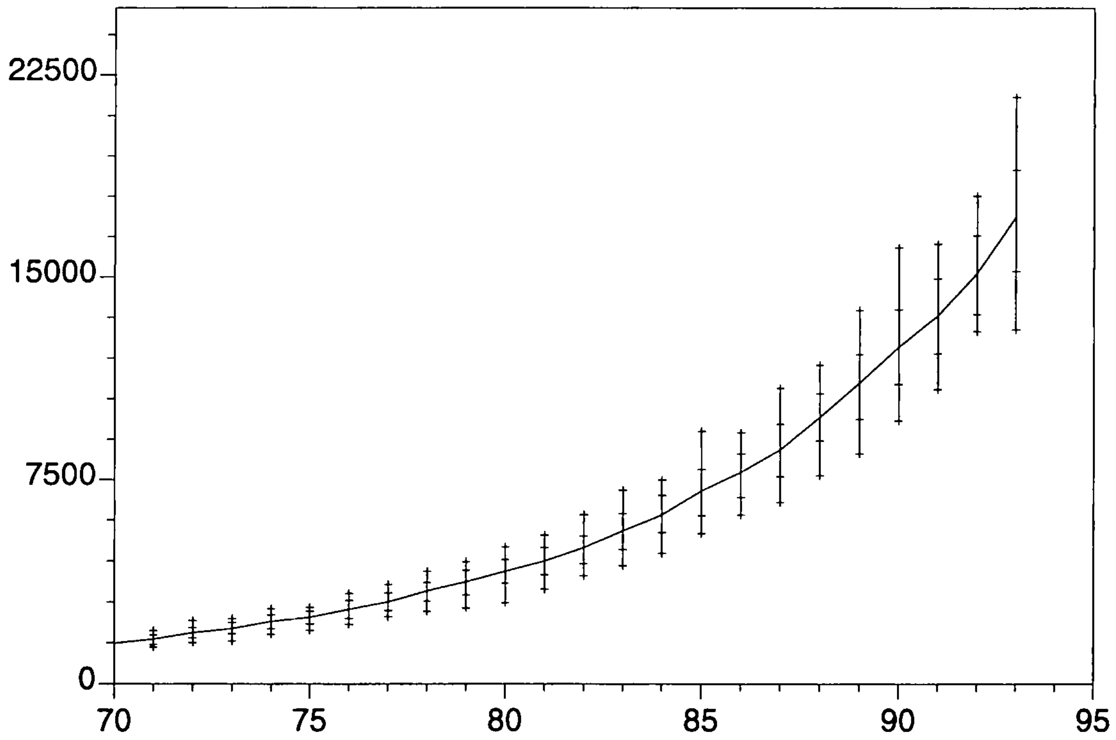
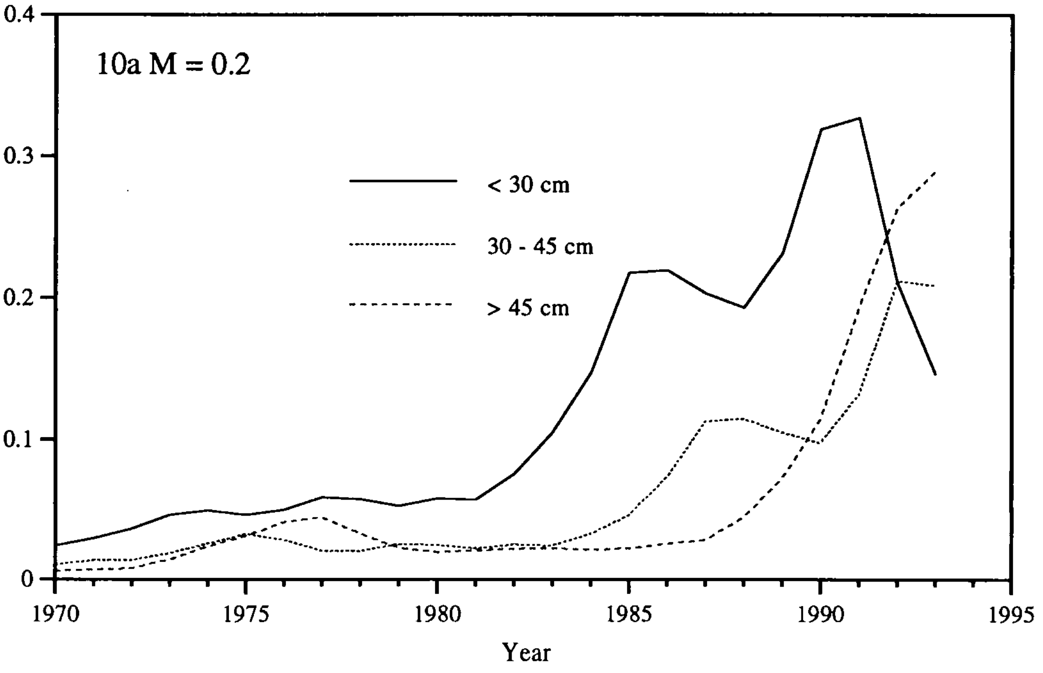


Figure 10. Average predation mortality of cod by grey seals by size class.



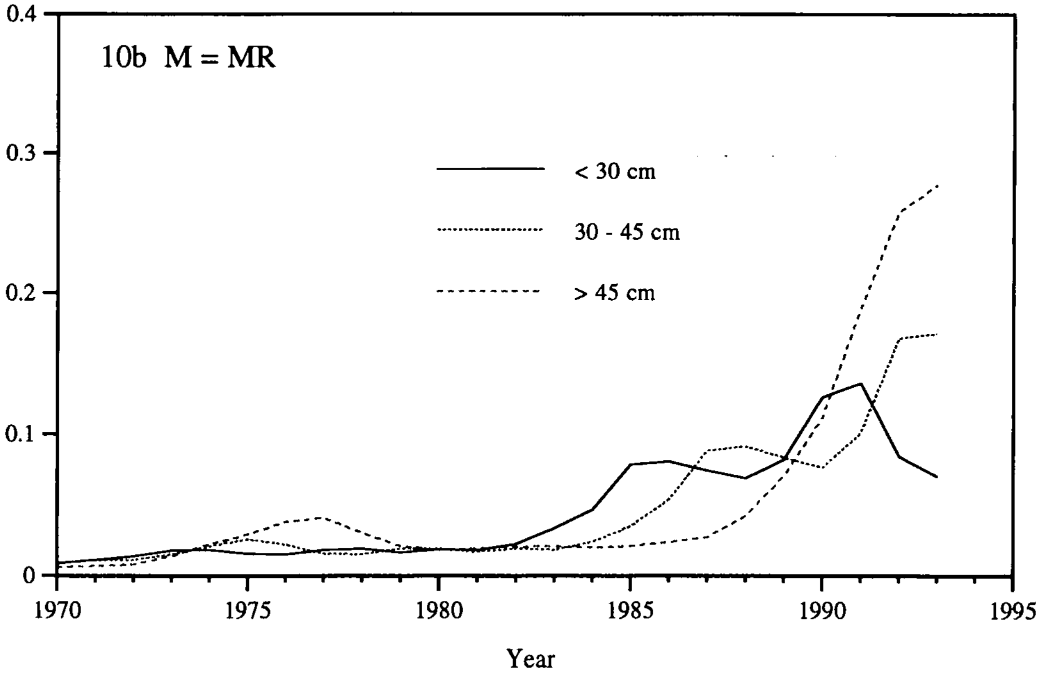


Figure 11. Cod mortality rates averaged over ages 2 - 8 with and without explicit seal predation.

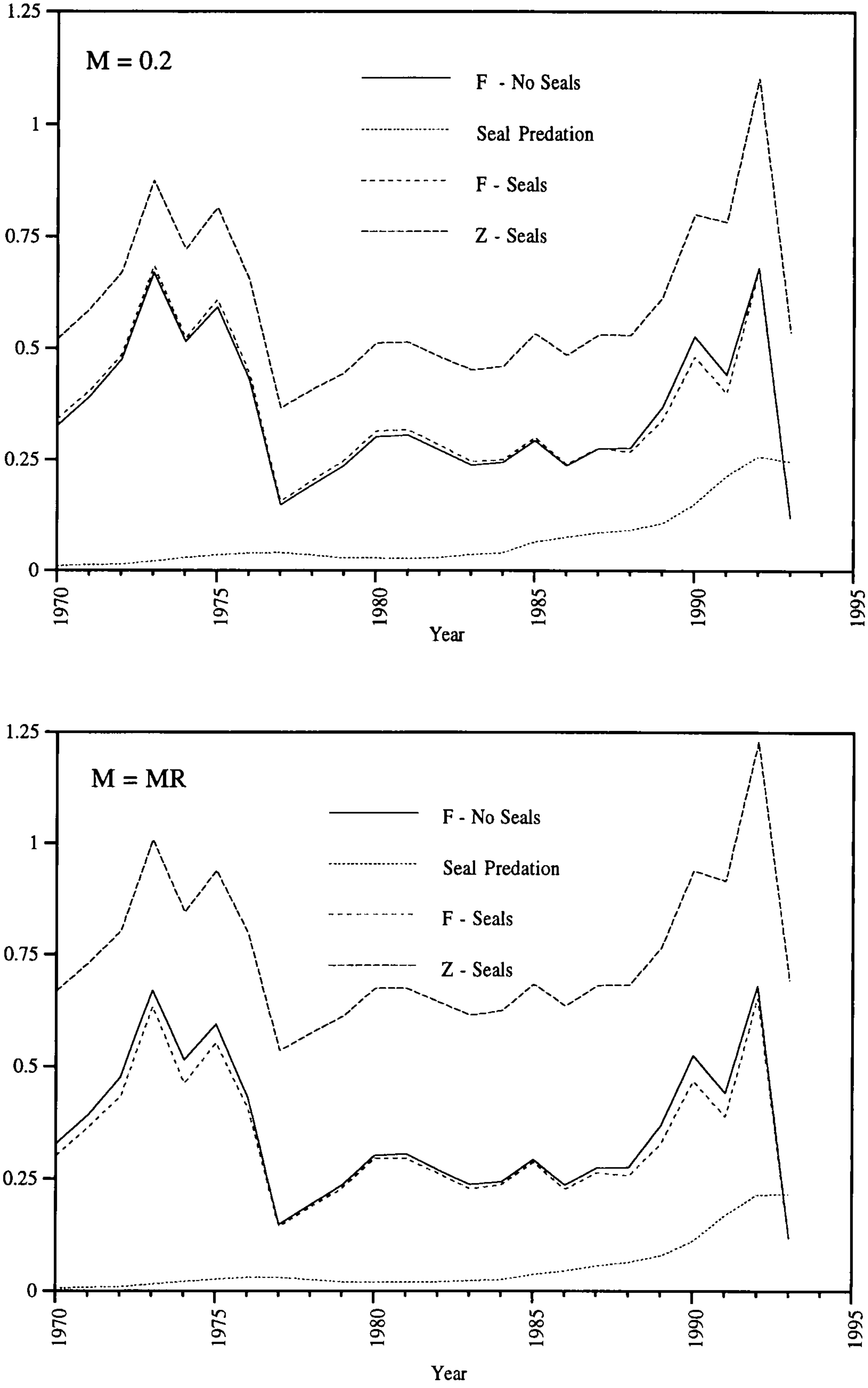


Figure 12. Recruitment series with (dashed line) and without (solid) seal predation. Note difference in scales between the two subplots.

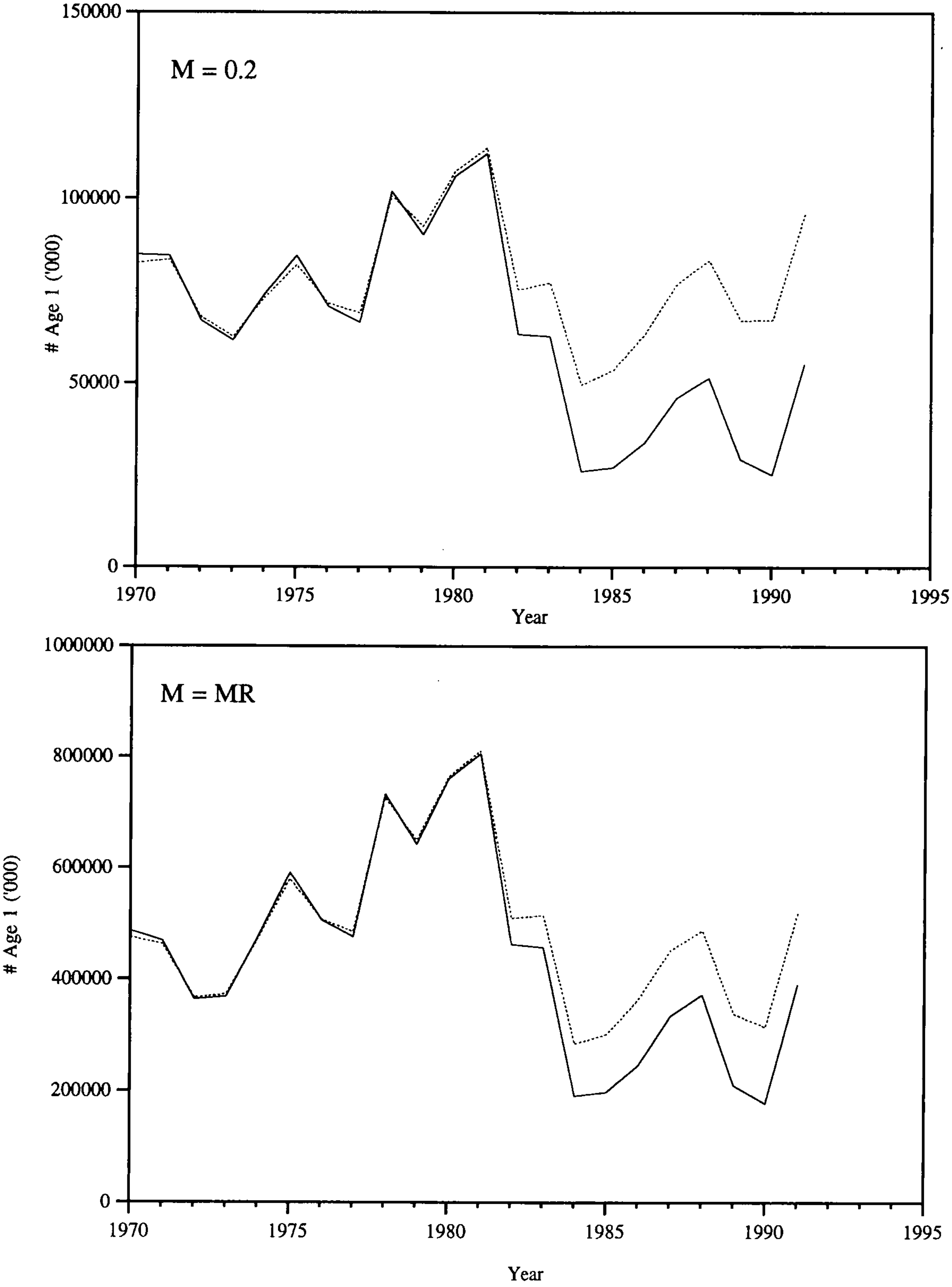


Figure 13. Effect of grey seal predation on 4VsW cod stock-recruit relationships. The year in each line is the locus without seal predation and the point is with seals.

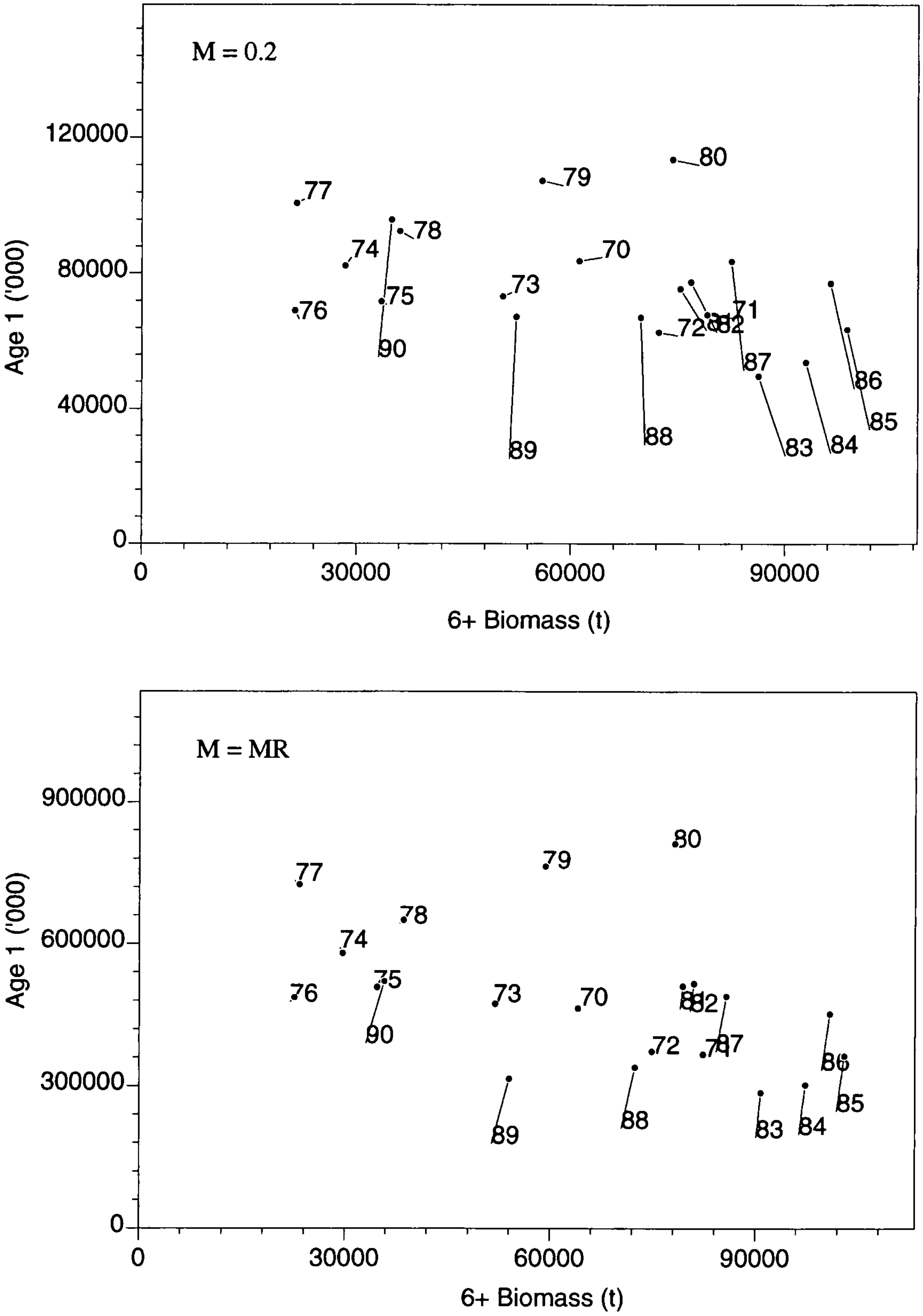


Figure 14. Effects of seal predation on yield per recruit analysis. The solid line is without seal predation and the three others include average predation for 1970 - 79, 1980 - 89 and 1990 - 1993.

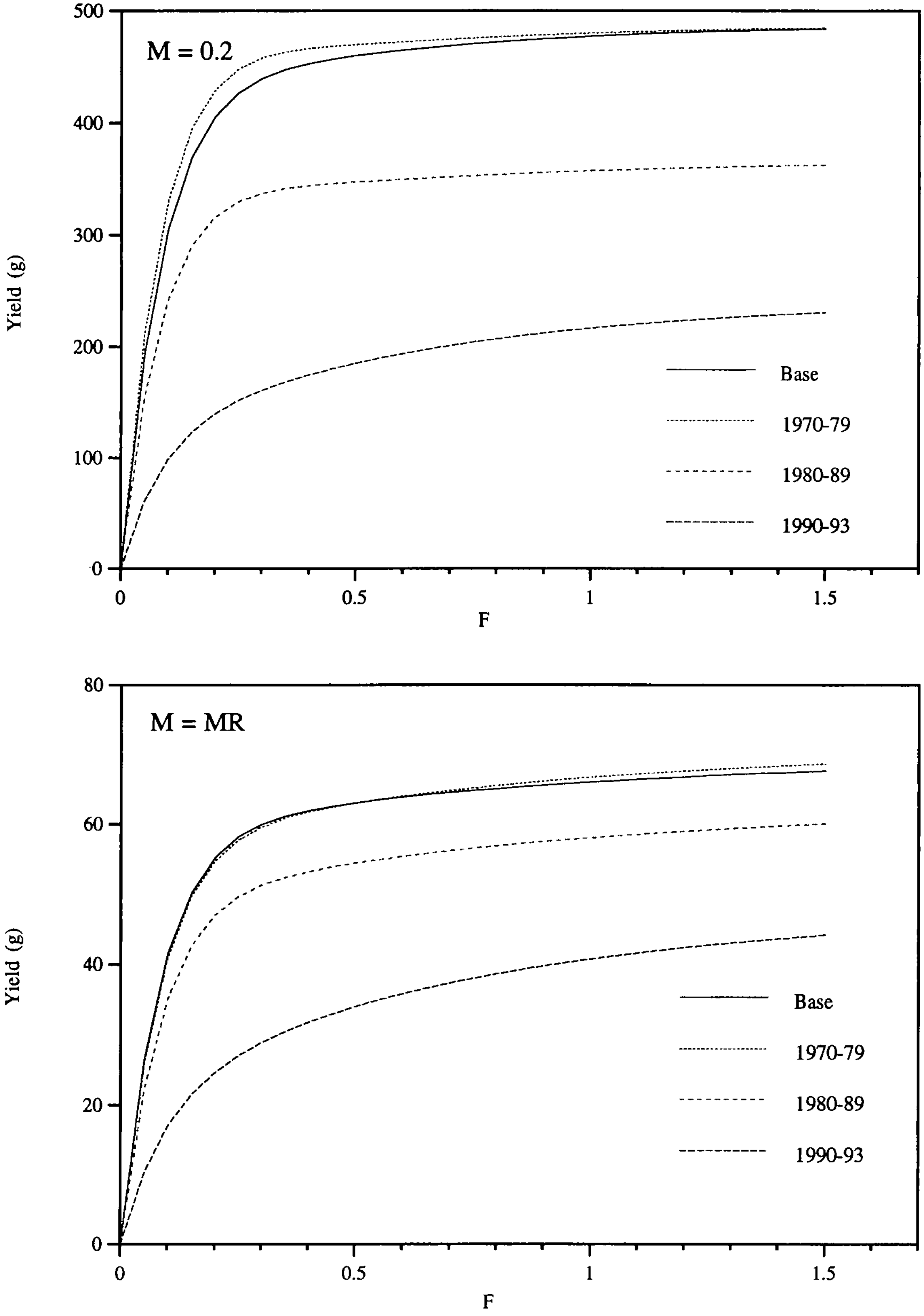
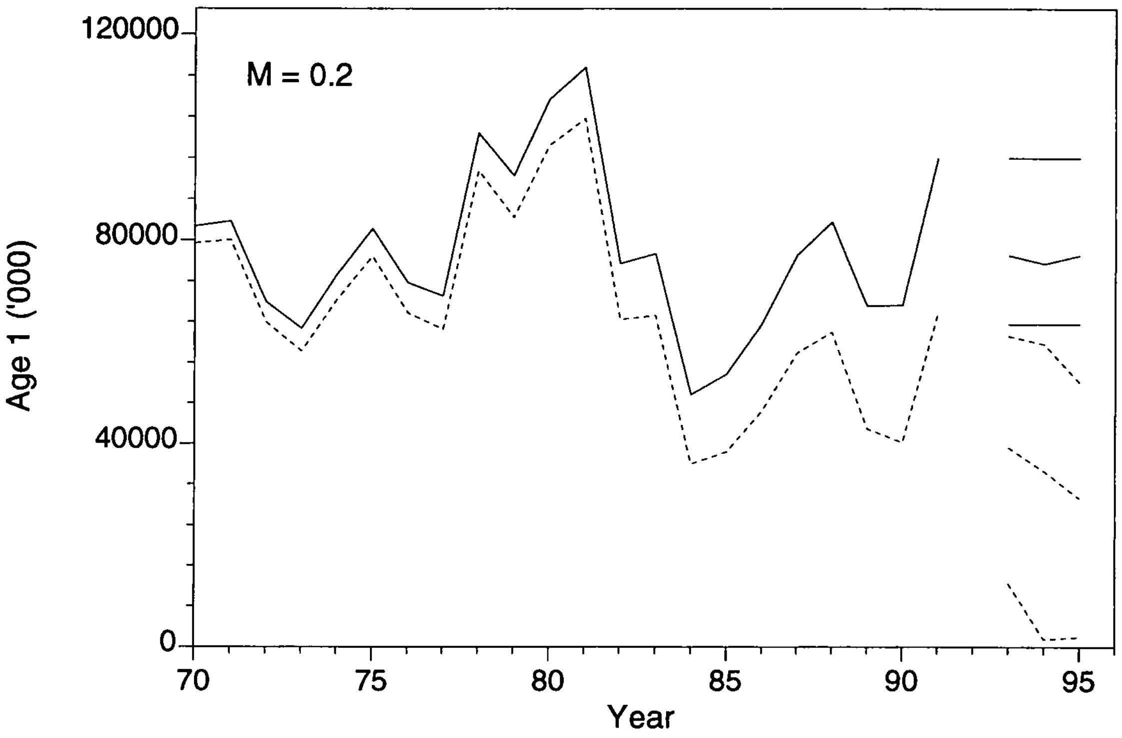


Figure 15. Historical and projected recruitment (solid) and recruitment minus the number of < 30 cm cod eaten by seals (dashed). The projection lines are bounded by ± 1 SD.



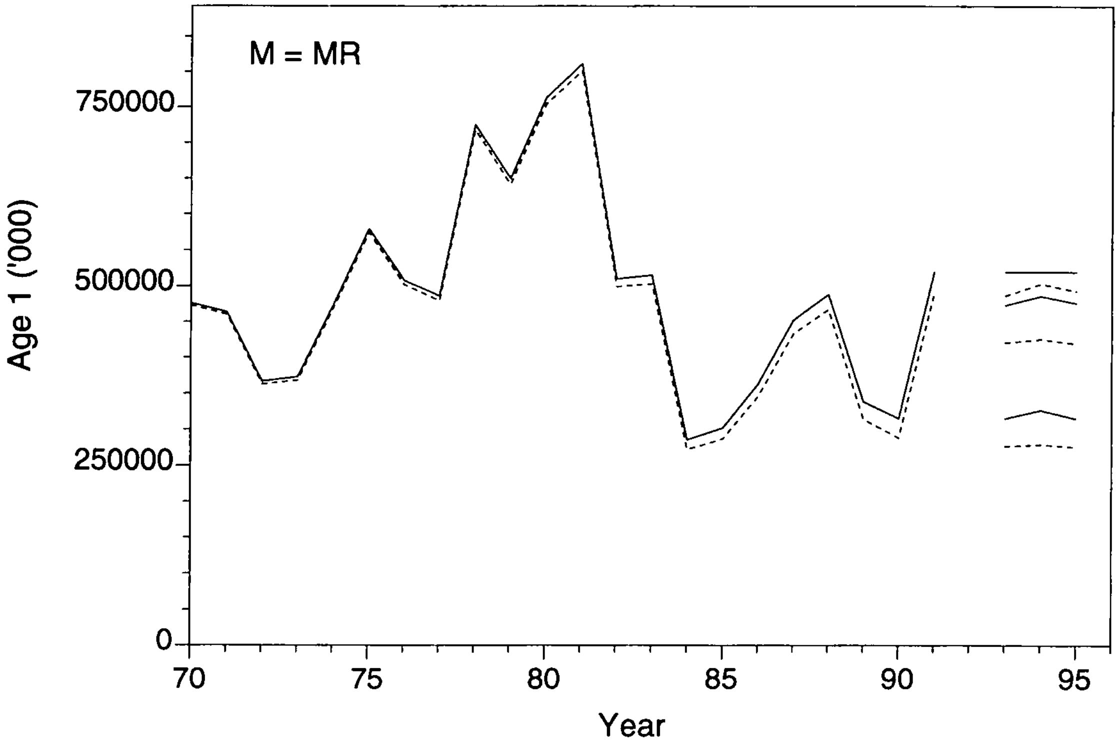


Figure 16. Two models for extrapolating 4VsW cod consumption by seals with 95% error bars from bootstrapping diets. The commercial landings are shown for comparison.