Grey seal predation on the eastern Scotian Shelf: modelling the impact on Atlantic cod

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Abstract: We modelled trends in the predation mortality of the Atlantic cod (*Gadus morhua*) stock on the eastern Scotian Shelf, Canada**,** by grey seals (*Halichoerus grypus*) and the potential effects of this mortality on cod recruitment over the period 1970–1994. Two predation models were explored: one in which the fraction of cod in the diet was constant and another in which the fraction of cod was proportional to cod abundance. The number of grey seals in the study area, from the Gulf of St. Lawrence and Sable Island populations, increased from about 5000 in 1970 to 64 000 in 1994, while total food consumption increased from 10 000 t·year^{-1} in 1970 to 121 000 t·year^{-1}. Under the constant ration model, grey seals consumed about 15 400 t of cod in 1994 compared with about 6300 t under the proportional ration model. Grey seal predation mortality was only 10–20% of estimated fishing until the fishery was closed in 1993, indicating that grey seals were not a major factor in the recent collapse of this stock.

Résumé : Nous avons modélisé les tendances de la mortalité du stock de morue franche (*Gadus morhua*) de l'est de la plate-forme néo-écossaise (Canada) due à la prédation par le phoque gris (*Halichoerus grypus*), et les effets potentiels de cette mortalité sur le recrutement de la morue pendant la période 1970–1994. Deux modèles de la prédation ont été explorés : dans l'un, la proportion de morue dans l'alimentation des phoques était constante, tandis qu'elle variait en fonction de l'abondance des morues dans l'autre. Le nombre des phoques gris présents dans la zone d'étude, qui appartenaient aux populations du golfe du Saint-Laurent et de l'île de Sable, a grimpé, passant d'environ 5000 têtes en 1970 à 64 000 en 1994, tandis que la consommation totale de nourriture passait dans la même période de 10 000 à 121 000 t·an^{-1}. Dans le modèle à ration constante, les phoques gris consommaient environ 15 400 t de morue en 1994 contre environ 6300 t dans le modèle à ration proportionnelle. La mortalité due à la prédation par le phoque gris correspondait à seulement 10–20% des prises commerciales estimées jusqu'à la fermeture de la pêche en 1993, ce qui permet de penser que ce pinnipède ne représentait pas l'un des facteurs principaux du récent effondrement du stock de morue.
[Traduit par la Rédaction]

Introduction

Seals are abundant predators in many marine ecosystems and as K-selected species may play a role in determining community structure (Estes 1979). Predation by seals also has the potential to reduce the yield from commercially valuable fish species (e.g., Beddington et al. 1985; Gulland 1987; Wickens et al. 1992), although as Estes (1979) observed there is little empirical data about "the roles of marine mammals in marine communities beyond poorly supported trophic arguments concerning marine mammal/fishery conflicts." Since Estes' paper was published, a number of estimates of food consumption by seal populations have been produced (e.g., Ashwell-Erickson and Elsner 1981; Anonymous 1984; Lavigne et al.1985; Ryg and Øritsland 1990; Olesiuk 1993; Perez and McAlister 1993; Ugland et al. 1993; Hammond and Fedak 1994), but fewer studies (Anonymous 1988; Sparholt 1990; Overholtz et al. 1991; Ugland et al. 1993) have attempted to estimate predation mortality or the impact of seal predation on fish population dynamics. In this paper, we develop a model to estimate trends in the consumption and resultant predation mortality by grey seals on the eastern Scotian Shelf (ESS) population of Atlantic cod (*Gadus morhua*) over the period 1970–1994.

The ESS Atlantic cod stock is located in NAFO subdivisions 4Vs and 4W off Nova Scotia, Canada (Fig. 1). Commercial landings of this stock 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 following a period of overexploitation. Landings increased to a peak of 50 000 t in 1985 as the stock rapidly recovered after fishing effort was reduced. The abundance and landings of the ESS cod stock have declined since the mid-1980s, reaching the lowest recorded level and closure of the directed fishery in 1993 (Mohn and MacEachern 1994). The causes for this latest dramatic decline in ESS cod abundance are poorly understood, but are thought to include high fishing mortality, unfavorable oceanographic conditions for cod growth and survival, and increased grey seal predation mortality (Fanning et al. 1995). The grey seal population in eastern Canada, and particularly that on the Scotian Shelf, has continued to increase over the last decade and has recently reached 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, Bedford Institute of Oceanography, Dartmouth, N.S., personal communication).
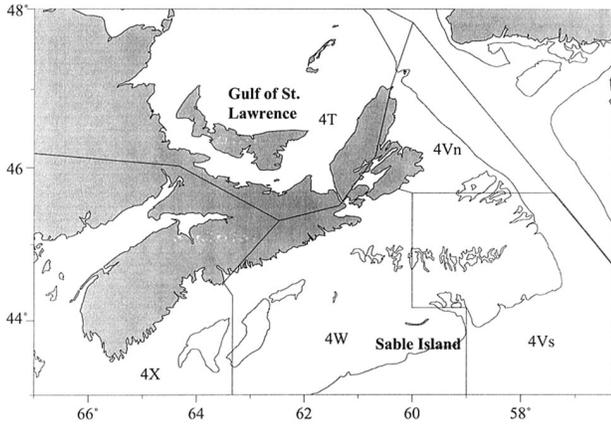
The grey seal is the most abundant pinniped species on the Scotian Shelf. The major grey seal breeding colonies in eastern Canada are located on Sable Island, in the western part of the study area (i.e., NAFO division 4W), and in the southern Gulf

Fig. 1. Eastern Scotian Shelf (NAFO subareas 4W and 4Vs) and southern Gulf of St. Lawrence (NAFO subarea 4T).

of St. Lawrence (Fig. 1, Mansfield and Beck 1977). Both juveniles and adults from these breeding colonies are known to disperse over large areas of eastern Canada during the nonbreeding season, but large numbers are known to feed on the ESS throughout most of the year (Mansfield and Beck 1977; Stobo et al. 1990). Some exchange of adults occurs between the two main breeding colonies, but the degree of mixing is estimated to be small (Zwanenburg and Bowen 1990). Although the genetic structure of the eastern Canadian population is unknown, we consider grey seals from each of these two areas as representing separate populations.

The objectives of this paper are to model the population dynamics of grey seals; estimate trends in the age-specific consumption of ESS cod by grey seals; estimate trends in grey seal predation mortality on three size-classes of ESS cod; compare annual estimates of grey seal predation mortality with estimates of fishing mortality on ESS cod; examine the effect of grey seal predation mortality on yield per recruit, the temporal pattern of the stock-recruitment relationship, and potential future recruitment of ESS cod; and explore the sensitivity of the model output to uncertainty in the model variables and assumptions.

Seal population models

Zwanenburg and Bowen (1990) used a Leslie matrix to model the dynamics of the Gulf of St. Lawrence (Gulf) and Sable Island (Sable) 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. We have built on the approach used by Zwanenburg and Bowen (1990) by constructing a deterministic, age-structured model, functionally similar to a Leslie matrix. The population numbers, $N[a;s;y]$, are described by a three-dimensional matrix having subscripts a, s, and y for age, sex (1 = male, 2 = female), and year, respectively. Thus, if the birth ogive is R, pup production in year y is

$$(1) \quad N[0;1;y] = N[0;2;y] = 0.5 \times \sum_a N[a;2;y] \times R[a]$$

In the present model, we used different rates of natural mortality in males and females after age 5 and different rates for the

Gulf and Sable populations. Reduced male survivorship has been inferred on the basis of 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 (e.g., Lander 1981; LeBoeuf 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 the observed longevity of males, we increased the mortality rate of males aged 6 years and older by a factor of 3 (Table 1). This approach is similar to that advocated by Barlow and Boveng (1991) in that we scaled mortality by longevity and used different rates for pups, juveniles, and adults. In the model, no grey seal survives beyond 39 years of age.

Estimates of grey seal pup production and age-specific birth and mortality (including hunting mortality) rates from several sources (see below) were used as inputs to the population models. Separate parameters were estimated for the two populations because of differences in the observed rate of increase in pup production between the Gulf and Sable components and because the Gulf population was culled during the breeding season between 1967 and 1983. Pup production estimates for both the Gulf and Sable Island populations were fit using a population projection model with two parameters. The first parameter scaled the fixed pattern of natural mortality and the second scaled the estimates of total population size in 1967. The two-parameter population model was then optimized with a nonlinear least squares (NLLS) fit (Press et al. 1988). The population age distributions in 1967 were then updated by taking the NLLS-derived rates of natural mortality and finding a stable age distribution. This distribution was then used to fit the two parameters again until the whole procedure stabilized. The resultant age-specific estimates of survivorship for males and females in the two populations are shown in Table 1.

Mid- to late-term pregnancy rates from Zwanenburg and Bowen (1990) were used as birth rates in the models (Table 2). These data are from Mansfield and Beck (1977) except that the Sable Island rate for females aged 6 years and older was increased to 91 to generate the observed rate of increase in Sable Island pup production (see Zwanenburg and Bowen 1990). We assumed that the age-specific birth schedule of both populations was constant over the period 1970–1994. Recent data collected in the Gulf of St. Lawrence (Hammill and Gosslein 1995) are similar to the earlier data presented by Mansfield and Beck, lending support for this assumption. We also assume that the age-specific mortality rates of the Sable population have remained constant. 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 clearly varied over time as a result of the cull on the breeding grounds between 1967 and 1984. In the model, these culls from the Gulf population were removed each year before natural mortality was applied.

Bootstrap estimates of confidence limits on population size

Bootstrapping (Efron 1982) is a computer intensive technique in which the underlying data or intermediate results are resampled,

Table1. Population parameters used to model the Sable Island and Gulf of St. Lawrence grey seal populations.

| | Mass (kg) | | Sable | | | Gulf | | |
| | | | M | | | M | | |
Age (years)	Male	Female	Male	Female	Birth %	Male	Female	Birth %
0	52	48	0.294	0.294	0	0.446	0.446	0
1	71	63	0.050	0.050	0	0.078	0.078	0
2	92	78	0.050	0.050	0	0.078	0.078	0
3	113	92	0.050	0.050	0	0.078	0.078	0
4	133	106	0.050	0.050	16	0.078	0.078	16
5	151	118	0.050	0.050	71	0.078	0.078	71
6	168	129	0.147	0.050	91	0.236	0.078	85
7	184	138	0.147	0.050	91	0.236	0.078	85
8	197	147	0.147	0.050	91	0.236	0.078	85
9	208	153	0.147	0.050	91	0.236	0.078	85
10	217	159	0.147	0.050	91	0.236	0.078	85
15	246	175	0.147	0.050	91	0.236	0.078	85
20	256	181	0.147	0.050	91	0.236	0.078	85
25	259	183	0.147	0.050	91	0.236	0.078	85
30	261	183	0.147	0.050	91	0.236	0.078	85
35	261	184	0.147	0.050	91	0.236	0.078	85
39	261	184	0.147	0.050	91	0.236	0.078	85

Note: M, instantaneous rate of natural mortality; Birth %, percentage of females giving birth.

the analysis is repeated, and the outputs are compiled. We bootstrapped the residuals (i.e., the differences between the data and the model predictions) to estimate confidence limits on the trends of both the Sable and Gulf populations. A sufficient number of replicates had been performed when the plot of estimated variance on population size versus the number of replicates reached an asymptote. Although this occurred after 30 replicates, we used 100 replicates to estimate the confidence limits for the two populations.

Trends in grey seal abundance

Figure 2a shows the estimated trend in Gulf pup production when the two-parameter model is fitted to mark–recapture estimates of pup production in 1984, 1985, 1986, 1989, and 1990 (Hammill et al. 1992). The two estimates for each of these mark–recapture studies were derived from independent samples of the ratio of tagged to untagged seals. The model shows that pup production in the Gulf increased slowly until the cull was ended in 1984. Thereafter, the population is estimated to have increased at about 9%/year, with a doubling time of about 8 years. The coefficients of variation (CV) on the estimates of Gulf pup production, from the NLLS fit, were 43 and 32% for initial population and natural mortality, respectively. Uncertainty in the estimated total numbers of Gulf grey seals increased markedly from the last pup production survey in 1990 (Fig. 2b). In 1994, the Gulf population was estimated at 68 700 seals, with a 95% confidence range of 42 000 – 100 000 (CV 22%).

Censuses of grey seal pup production on Sable Island were attempted in most years between 1962 and 1990 (Mansfield and Beck 1977; Stobo and Zwanenburg 1990). However, counts prior to 1976 were often based on short visits to the island and, in most cases, underestimated pup production (Zwanenburg and Bowen 1990). Thus, we used only pup censuses conducted between 1976 and 1990 (Stobo and Zwanenburg 1990) to estimate the trend in Sable Island pup production

Table2. Age-specific, late-term pregnancy rates of grey seals from Mansfield and Beck (1977) used as birth rates in the model.
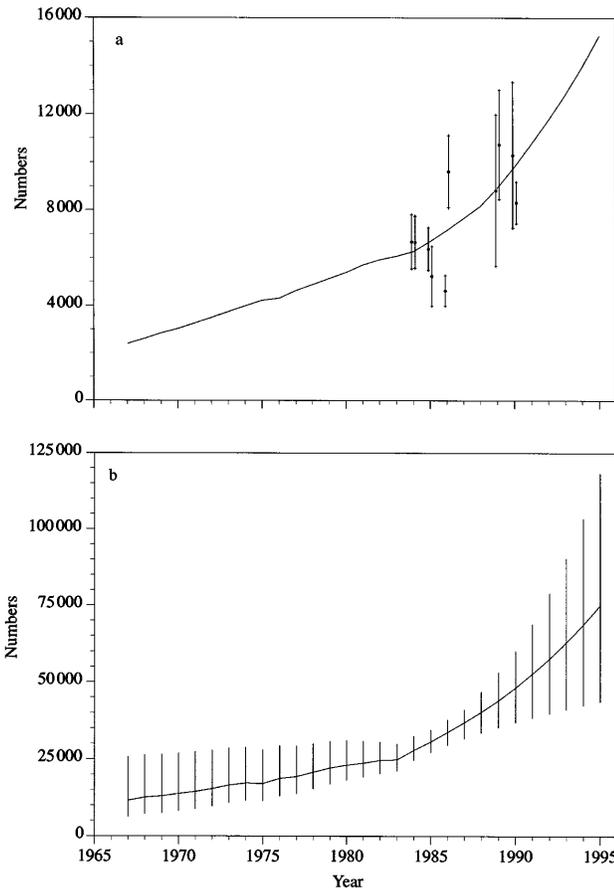
Age (years)	Number pregnant	Total number	% pregnant
4	3	19	17
5	5	7	41
6+	43	50	86

during the period 1967 to 1994. Pup production estimates prior to 1976 lay consistently below the line as previously reported (Fig. 3a). The CVs for the parameter estimates of the Sable Island pup production model were 9 and 7% for starting population and natural mortality, respectively. A preliminary estimate from the 1993 aerial photographic survey (W.T. Stobo, personal communication, see Fig. 3a) indicates that pup production on Sable Island continues to increase at about 13%/year. This corresponds to a doubling time of slightly less than 6 years. The Sable population in 1994 was estimated at 85 300 (78 000 – 95 000 95% confidence interval; CV 4%) seals (Fig. 3b).

Our analysis suggests that the Gulf and Sable populations have experienced different dynamics over the past three decades, such that there has been a shift in the relative contribution of these populations to the total number of grey seals in eastern Canada. In 1970, we estimate that 73% of the total population was of Gulf origin. By 1982, the two populations were about equal in numbers. However, by 1994, only 45% of the estimated total population (about 154 000 seals) was of Gulf origin.

The dynamics of these two populations over the past several decades are described reasonably well by the two-parameter model. Pup production and hence our estimates of trends in the Gulf population size are much less certain than they are for Sable Island. However, neither population can continue to increase exponentially indefinitely. At some point, density-

Fig. 2. Estimates and model fit (solid line) of pup production (*a*) and total population size (*b*) of Gulf of St. Lawrence grey seals with 95% confidence limits estimated by bootstrapping.

Fig.3. Census counts and model fit (solid line) for pup production (*a*) of the Sable Island grey seal population. Only data from 1976–1990 (dots) were used to estimate model parameters. Preliminary aerial survey estimate for 1993 also shown. (*b*) Trend in total population size of Sable Island grey seals with 95% confidence limits estimated by bootstrapping.
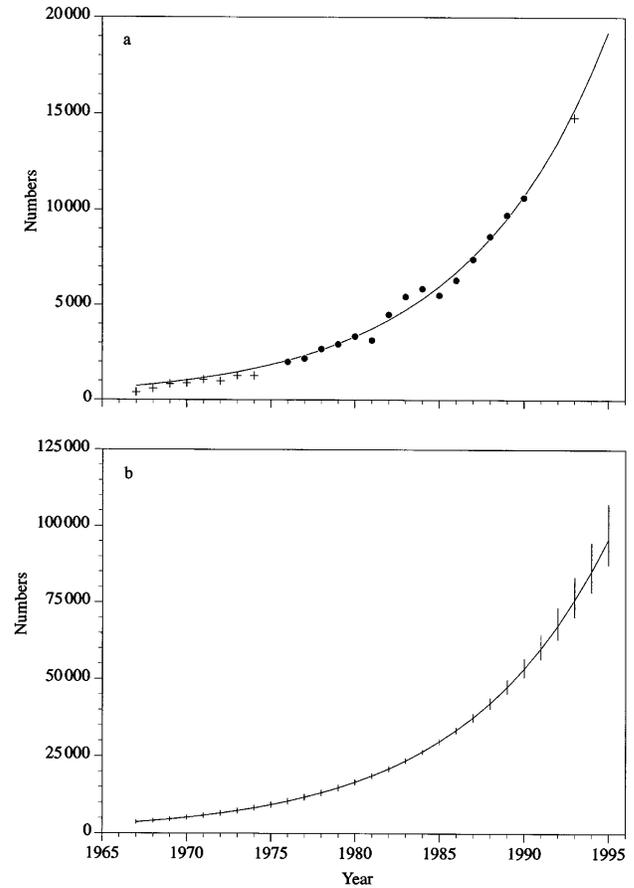
dependent changes in population parameters will alter current population trajectories. We have not considered density dependence in this study, as the empirical evidence suggests that this factor has not affected the dynamics of these populations.

Seasonal distribution of grey seals in the 4VsW study area

The magnitude of grey seal predation on ESS cod depends, among other things, on the seasonal distribution of grey seals, as the two grey seal populations are known to undertake wide-ranging seasonal movements (Mansfield and Beck 1977; Lavigueur and Hammill 1993; Stobo et al. 1990). The relative contributions of both populations to the total number of grey seals in the study area (Table 3) were derived from a qualitative assessment of the seasonal distribution of tag recoveries from seals marked in the Gulf and on Sable Island (Lavigueur and Hammill 1993; Stobo et al. 1990) and from a general knowledge of the natural history of grey seals where tag return data were clearly deficient. For example, tag recoveries are mainly from coastal locations and from pups and juveniles. Thus, they provide little information on the offshore distribution of grey seals or the distribution of adults, particularly during the breeding season.

Table3. Percentage of each population of grey seals in the ESS study area by quarter of the year. First quarter begins January 1.

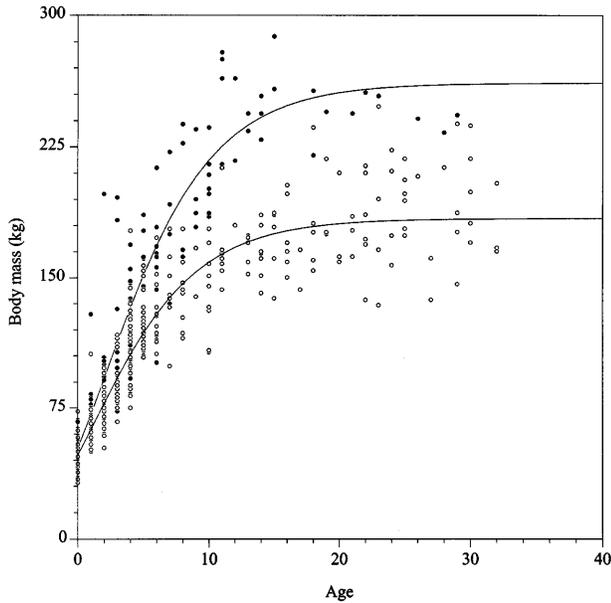| Population	Quarter			
	1st	2nd	3rd	4th
Sable	90	50	50	80
Gulf	10	20	20	10

Predation models

Seal energy requirements

Estimates of the average daily metabolic rate (ADMR) of free-living grey seals are not available. Castellini et al. (1992) measured the metabolic rates in five free-living, adult Weddell seals (*Leptonychotes weddellii*) while the animals were resting, while they were diving, and during sleep and found that their ADMR was 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

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Fig. 4. Gompertz growth models fit to male (solid circles) and female (open circles) grey seal body masses collected from the Gulf population.

Table 4. 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

feeding, and $3.4 \times BM^{0.75}$ is the Klieber equation. The estimated ME in grey seals fed herring averaged $83 \pm 4.8\%$ of gross energy intake (Ronald et al. 1984). There are no estimates of the HIF in grey seals. Instead, we used recent data from captive harbour seals showing that an average of 8.3% of GEI is lost to HIF (Markussen et al. 1994). Although it could be argued that HIF is accounted for in the Klieber multipler of 2, we identified HIF as a term in the equation so that we could assess the sensitivity of our estimates to variation in this parameter.

We made a number of simplifying assumptions in calculating the energy requirements of the two grey seal populations. In particular, we did not explicitly account 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 and for a number of these parameters little information exists. Therefore, the inclusion of such detail in many cases results in a loss of precision in the model. Also, although reproduction is costly, much of this expense is cancelled by the reduced energy requirements during the moult (Ryg and Øritsland 1991). Finally, 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).

The age-specific body masses of male and female grey seals were determined from samples collected in the Gulf of St. Lawrence between 1988 and 1992 (M. Hammill, Maurice Lamontagne Inst., Mont Joli, Que., unpublished data) (Fig. 4). These data were fit using an NLLS and the Gompertz equation in the form

(3) $BM = p_1 \times \exp(p_2(1 - \exp(-p_3 \times a)))$

where BM and a are as defined previously and p_1–p_3 are parameters to be estimated. These growth curves (Table 4) were used for both the Gulf and Sable Island populations.

Preysize and composition of greyseal diets
The percent wet mass of ESS cod and other prey in the diet of grey seals was estimated from otoliths and other hard parts recovered in 198 grey seal stomachs from inshore sites along the eastern shore of Nova Scotia and 393 faecal samples collected on Sable Island during 1988–1993 (Bowen et al. 1993; Bowen and Harrison 1994; W.D. Bowen, unpublished data; Table 5). Atlantic cod constituted 1.6–44.1% by mass of the diet in the above studies. Although these estimates varied considerably, there was little evidence of an interannual trend in the percentage of cod in the diet despite marked variation in the abundance of ESS cod over the same time period. The average energy density of the 13 diet samples varied from 5.0 to 8.8 kJ/g wet mass.

There are no quantitative data on grey seal diets on the Scotian Shelf prior to 1988. Although estimates of percent wet mass are not available, we do have frequency of occurrence

equation. Fedak and Hiby (in Anonymous 1984) measured the metabolic requirements of 10 grey seals ranging in age from 1 month to more than 10 years and in body mass from 43 to 270 kg. They estimated that an adult grey seal would expend energy at a rate about twice that predicted by the Klieber equation. Although these data do not include the cost associated with diving, both the Weddell seal results and recent studies on free-ranging grey seals that demonstrate marked reduction in heart rate during diving (Thompson and Fedak 1993; Fedak and Thompson 1993) suggest that the ADMR of adult grey seals is reasonably estimated at two times the Klieber equation.

The mass-specific metabolic requirements of young growing animals are greater than those of adults. Lavigne et al. (1986) concluded that the standard metabolic rate of immature, growing pinnipeds was about two times that predicted by Klieber's equation for adults. Worthy (1987) found that most values of standard metabolic rate in captive, neonatal grey seals lie between two and three 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 the rate predicted by Klieber's equation, respectively. We have assumed that metabolic rate decreases geometrically to the adult rate (i.e., age 6 and older), such that pups through 5-year-old seals require a premium of 200, 150, 125, 112, 106, and 103%, respectively.

We used the following equation to estimate the daily gross energy intake (GEI; in watts per day) of an individual grey seal:

(2) $GEI(s,a) = GP(a) \times (2 \times 3.4 \times BM(s,a)^{0.75})/$
$(ME - HIF)$

where s is sex and a is age (0–39 years for males and females), GP is growth premium, BM is body mass (kg), ME is metabolizable energy (i.e., the proportion of GEI available to the animal), HIF is the proportion of GEI lost to heat increment of

Table 5. Estimates of percent wet mass and energy density of grey seal diets from stomachs and scats collected on the Scotian Shelf from inshore (in) and offshore (off) locations in 1988–1993.

	1988–1990 Summer (In)	1988–1990 Summer (Off)	1988–1990 Winter (In)	1988–1990 Winter (Off)	1992 (summer) (in)	1991 July (off)	1991 Sept. (off)	1991 Nov. (off)	1992 Feb. (off)	1992 Mar. (off)	1992 May (off)	1992 Aug. (off)	1993 (Jan.) (off)	Energy kJ/g	Energy 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	4.2	1
Haddock					2.6									5.4	2
Pollock	7.0	6.8												5.0	3
Redfish						1.2		0.4	2.7	2.4	0.7	1.5	0.4	4.2	1
Silver hake	3.2	25.8	0.7	0.6	2.5	5.0	3.1	1.5	0.4	0.2	0.1	5.6		4.2	1
Flatfish					14.6	18.5	2.9	7.8	10.7	15.7	19.4	7.5	7.9	4.2	1
Sand lance		32.7		75.1		56.0	49.7	75.1	78.7	76.1	77.8	67.2	85.3	6.7	4
Herring	65.8		9.0		33.2									10.9	2
Mackerel	0.4		47.4		9.9									10.0	5
Squid	1.4	26.6	12.9	4.2										4.2	5
Total	95.4	98.0	83.9	100	96.3	99.7	99.8	97.5	96.0	98.5	99.6	99.0	97.3		
Average energy	8.8	5.0	8.4	6.3	7.1	5.4	5.4	6.3	6.3	6.3	6.3	5.9	6.3		
Sample type	Stom	Stom	Stom	Stom	Stom	Scat	Scat	Scat	Scat	Scat	Scat	Scat	Scat		
n	90	26	16	11	55	50	52	49	41	54	43	59	45		

Note: Stom, stomach sample. Source: 1, W.D. Bowen and S.J. Iverson, unpublished data; 2, Murie and Lavigne (1992); 3, Jensen (1979); 4, Birkhead and Nettleship (1987); 5, Bowen et al. (1993).

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

Years	Location	% relative frequency of occurrence of cod	Source
1969–1971	Atlantic Canada	16.9	Mansfield and Beck 1977
1963–1987	Nova Scotia	3.6	Benoit and Bowen 1990
1983–1984	Sable Island	21.3	Benoit and Bowen 1990

data from eastern Canada for earlier periods (Table 6). These data indicate that cod was frequently consumed by grey seals from 1970 to 1993. Frequency of occurrence data underestimate the importance of cod in the diet of grey seals compared to relative percent wet mass (Benoit and Bowen 1990; Bowen et al. 1993). Thus, these limited data suggest that cod may have represented a larger fraction of the grey seal diet in the past, when ESS cod were more abundant. We used this observation as a rationale for the development of the proportional ration model.

Our estimates of diet composition are based mainly on the identification of otoliths and squid beaks. Undigested prey are occasionally found in stomachs, but they constitute <1% of the reconstructed mass of food eaten. Prey without hard parts and those with hard parts that are not resistant to digestion will be underestimated in the diet by this method. This will tend to overestimate the importance 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, we have adjusted the average energy of the diets given in Table 5 on the assumption that 20% of the diet by mass may not have been seen. We assumed that the average energy density of this unseen prey was 4.2 kJ/g wet mass, a value that would be

appropriate for squid and small gadoids and flatfishes whose otoliths are unlikely to survive digestion (Table 5).

The relationships between otolith length and body length of ESS cod and other prey were used to estimate the size of prey consumed by grey seals (Bowen et al. 1993; Bowen and Harrison 1994). We used three length-classes of cod in our analysis (<30, 31–45, and >45 cm). The average mass and length at age of Atlantic cod were determined from groundfish bottom trawl surveys conducted over the period 1970–1993 (Mohn and MacEachern 1994). The cut points of the three length-classes (30 and 45 cm, Table 7) fell midway in the length distribution of the 2 year olds and the 4 year olds, respectively, as determined from the July groundfish survey. The proportion by number of cod at age, within a size-class, was used to estimate the average mass for each of the three size categories: 0.12, 0.50, and 1.80 kg, respectively (Table 7). These masses were multiplied by the percentages of cod for each size category (79, 16, and 5%) from the seal diet studies (Bowen et al. 1993; Bowen and Harrison 1994) to give the percentage by mass (36, 30, and 34%) of cod in the diet. In the model, we assume that the percentage in each of these three length-classes of ESS cod eaten by grey seals is constant over time, although the percentages would change owing to varying year-class strengths and variation in growth. To convert the removals by seals from the three length categories into age categories the process was essentially reversed. The numbers eaten in each size category were partitioned into age-classes according to the proportions in the first three columns of Table 7.

Models of seal food consumption on the eastern Scotian Shelf

The functional response of grey seals to changes in prey abundance is unknown. Therefore, we use two models to describe ESS cod consumption by grey seals. We call these the constant ration and the proportional ration models. The constant ration model assumes that there is sufficient prey such that ESS cod

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Table7. Proportion of numbers in each length category and mean length and mass at age of ESS cod from July bottom-trawl roundfish surveys.

Age (years)	Length category			Mass (kg)	Length (cm)
	0–30 cm[a]	31–45 cm[a]	>45 cm[a]		
1	0.75	0.00	0.00	0.08	20.3
2	0.25	0.39	0.00	0.25	29.1
3	0.00	0.47	0.00	0.56	38.2
4	0.00	0.14	0.27	0.98	46.2
5	0.00	0.00	0.33	1.51	53.5
6	0.00	0.00	0.20	2.10	59.8
7	0.00	0.00	0.12	2.78	65.6
8	0.00	0.00	0.07	3.75	72.2

[a]Derived from smoothed average survivorship of cod from the VPA.

represent a constant fraction of the grey seal diet irrespective of the abundance of ESS cod. Although this might seem to be an unrealistic model, cod comprise only a small fraction of the diet and thus grey seal predation may not be closely coupled to the abundance of cod. In fact, our data on the percentage of cod in the diet of grey seals between 1989 and early 1993 suggest this relationship (Table 5). In the second model, we assume that grey seal predation is proportional to the biomass of ESS cod (similar to a Lotka–Volterra relationship), that is

$$(4) \quad E_s = q_s \times B_s \times N'$$

where E_s is the mass (tonnes) of cod eaten in size-class $s = 1–3$, B_s is the estimated 4VsW cod biomass in the three length-classes, q_s is a scaling coefficient, and N' is the number of seals scaled by age and sex for their energy requirements. By finding the average cod biomass (3875, 21 725, 65 650 t for cod length-classes 1–3, respectively), the amount eaten by seals (3367, 2806, 3189 t), and the average number of seals (38 730) in 4VsW over the 4-year period (1989–1992) covered by the diet study, the average q_s values are determined (2.25, 0.33, 0.12; $\times 10^{-5}$). These q_s values 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. This model essentially assumes that the availability of all other food items is irrelevant and that when the cod biomass doubles, its abundance relative to other prey also doubles. This assumption is required because the abundance of most other prey is not known.

Grey seal predation on each length-class of cod and the total biomass of prey consumed were estimated quarterly. The fractions of the Gulf and Sable grey seal populations in the study area each quarter were taken from Table 3. The percentages of ESS cod in the diet were then calculated depending upon the ration model chosen. The values for each of the length-classes of ESS cod in the diet were converted from tonnes into numbers of fish as described above using the values in Table 7. Daily GEI of the grey seal population was calculated for each sex by multiplying numbers of seals at age corrected for survivorship by the appropriate GEI(s, a) and then summing over ages. The daily GEI was converted from mass of food eaten into a quarterly energy requirement in tonnes by dividing the requirements by the average energy density of the prey (Table 5) and summing over the number of days per quarter. We use population numbers in 1994 as an example of the age- and sex-specific daily energy requirements, and daily and annual

food consumption of grey seals (Table 8). Because of the effect of the growth premium on energy requirements and, more importantly, because of the greater abundance of younger seals, the first five age-classes (ages 0–4) represent over half the population food consumption.

The total annual food intake by grey seals in the study area increased from an estimated 10 000 t (8100 to 12 600 95% CI) in 1970 (rounded to the nearest 1000 t) to 121 000 t (112 000 to 133 000 95% CI) in 1994. In the constant ration model, the assumption that 20% of the diet was unseen decreased the percentage of cod in the diet by 25% and the total energy intake by about 8%, resulting in an increase in quarterly food intake of about 9%. For example, the estimated quarterly food intake of a 4-year-old male would increase to 0.59 t after the correction for unseen prey from 0.54 t before the correction. On average, approximately 15% of the adjusted grey seal diet was cod.

The estimated biomass of ESS cod consumed by grey seals in the constant ration model increased steadily from an average of about 1250 to 15 400 t over the period 1970–1994 (Fig. 5). In the proportional ration model, the estimated consumption of ESS cod by grey seals was low in 1970, increased to a peak during the period of high cod abundance during the early 1980s, and then gradually declined to about 6300 t in 1994 (Fig. 5). The directed fishery for cod was closed in September 1993 and the 1994 landings were less than 400 t.

The same overall patterns are observed when both landings and grey seal predation on cod are expressed in terms of numbers of fish. Under the constant ration model, grey seals are estimated to have consumed about 5 million ESS cod in 1970, increasing to about 60 million cod by 1994, comprising mostly fish <30 cm in length. By contrast, under the proportional ration model, grey seals consumed about 25 million ESS cod in 1970, about 53 million during the early 1980s, and about 23 million cod in 1994.
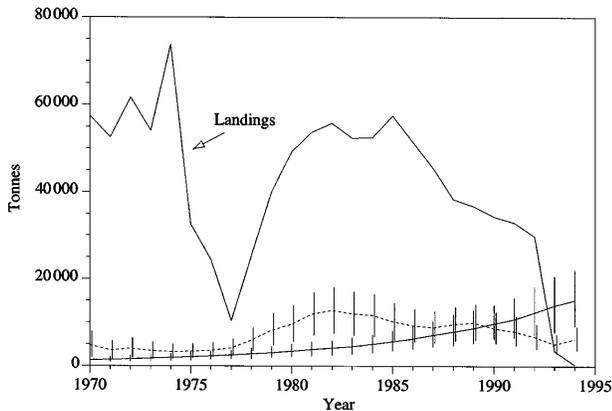
Sensitivity and uncertaintyof the predation model

Our estimates of grey seal predation mortality on cod depend on the precision of the data used in the model (i.e., sampling error) and the validity of our assumptions where data are unavailable (i.e., model error). We used two approaches to assess the sensitivity of model estimates to uncertainty in input parameters: bootstrapping and changing the magnitude of input parameters. For the food consumption models, bootstrap experiments were performed that explicitly resampled the underlying data. To assess the contribution of components of the bioenergetic equation (eq. 2) to uncertainty in food consumption, we bootstrapped data on the percentage of cod in the diet ($n = 13$, Table 5), the average energy density of the diet ($n = 13$, Table 5), the heat increment of feeding ($n = 19$, Markussen et al. 1994), and metabolizable energy ($n = 9$, Ronald et al. 1984). Variation in grey seal mass at age from the growth model (Fig. 5) was estimated by conditioned bootstrapping (100 replicates) on the residuals from the Gompertz model. The variance in the total food consumption was most affected by the average energy of the diet, about a 4% CV (Table 9). When all the sources were resampled the CV of the total food consumption was 5.1%. The CV for the amount of cod eaten was about 21% when the percentage of cod in the diet was bootstrapped and less than 5% for the other parameters. When

Table 8. Age- and sex-specific numbers, daily energy intake, daily food intake, and annual food intake of the grey seals in the study area in 1994.

Age (years)	Number in 1994		Daily energy per individual (W)		Daily food per individual (g)		Annual population consumption (t)	
	Male	Female	Male	Female	Male	Female	Male	Female
0	5 658	5 658	353	331	5028	4723	10 391	9 760
1	4 365	4 365	335	304	4777	4335	7 616	6 911
2	3 701	3 701	338	298	4816	4245	6 509	5 738
3	3 136	3 136	354	305	5052	4348	5 787	4 981
4	2 657	2 657	378	319	5384	4543	5 225	4 409
5	2 250	2 250	405	336	5777	4795	4 748	3 940
6	1 812	1 907	426	349	6075	4974	4 021	3 463
7	1 391	1 622	454	368	6478	5244	3 292	3 106
8	1 068	1 379	478	384	6822	5471	2 660	2 756
9	818	1 170	499	397	7112	5659	2 124	2 419
10	626	994	516	408	7354	5815	1 683	2 111
15	163	433	565	439	8059	6255	481	990
20	43	191	583	449	8311	6406	130	447
25	11	85	589	453	8398	6456	35	200
30	3	39	591	454	8428	6473	9	92
35	1	17	592	454	8438	6478	2	40
39		9	592	454	8441	6480		21
Total	29 486	34 270	534[a]	420[a]	7622[a]	5984[a]	59 837	61 943

[a]Column average.

Fig. 5. Commercial landings (t) and biomass (t) of ESS cod eaten by grey seals with 95% error bars for the constant (solid line) and proportional (broken line) ration models.

Table 9. Bootstrap coefficients of variation (%) for components of the grey seal consumption model.

Parameter sampled	Total consumption	Cod consumption
% cod eaten	1.0	20.9
Average energy of diet	3.9	3.9
HIF	1.0	1.0
ME	2.1	2.1
Gompertz parameters	1.5	1.5
All of the above	5.1	22.2

the proportional change of an output (O) divided by the proportional change of a parameter or intermediary variable (X) and expressed as a percentage:

$$(5) \quad R = 100 \times (\Delta O/O)/(\Delta X/X)$$

First, a base run was made with unperturbed parameters and the outputs, cod and total consumption in 1994, were estimated. Then, one of the parameters, for example the HIF, was increased by 10%. The model was run again and the amount of cod and total prey consumed were then compared with the base run and the relative difference was computed. In this example the relative sensitivity was 26% for either cod or total consumption.

The estimated cod consumption by grey seals was quite sensitive to the size of the Sable Island population, the fraction of GEI available to the animal, the percentage 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 were relatively insensitive to a change in the size of the Gulf population. However, the quarterly distribution of the two populations was quite uncertain and this uncertainty translated directly into uncertainty in the effective population size and

all five sources were resampled together the CV on the amount of cod eaten per seal was about 22%.

The error bars in Fig. 5 combine the uncertainty in the estimation of both population size and the percentage of cod in the diet, under the constant ration and proportional ration models. When both sources of uncertainty were bootstrapped, the CV of food consumption by grey seals was 23.1%. When only the percentage of cod in the diet was bootstrapped, the CV was 22.3%, illustrating the importance of this source of uncertainty for estimates of cod consumption. The contribution from the variance in the population alone was 5.4%.

The sensitivity of the model to various parameters or state variables was examined by independently changing parameters used in the predation model by 10% (Table 10). The measure we used is known as the relative sensitivity (R), which is

Table10. Relative sensitivity (%) of cod and total annual food consumption to a 10% increase in input parameters.

Parameter	Base value	Cod consumption	Total consumption
Sable numbers	Fig. 3	83	83
Gulf numbers	Fig. 2	17	17
% Sable in ESS, 2nd quarter	50	15	15
% Gulf in ESS, 2nd quarter	20	6	6
% unseen prey	20	–9	7
Growth premium	See text	63	63
ME	0.83	–112	–112
HIF	0.083	26	26
% cod in diet	15.2	100	0
Average energy density of diet	1.45	–83	–83
Klieber multiplier	2	100	100
Seal mass at age	From Table 1	74	74

Table11. Summary of yield per recruit and potential yield estimates of the 1990 year-class of ESS cod for two types of natural mortality (M_C and M_{AS}) and with or without predation by seals.

	M_C		M_{AS}	
	No seals	Seals	No seals	Seals
Recruits in 1990 year-class (millions)	25	72	183	303
F0.1*	0.174	0.480	0.174	0.481
Yield per recruit at F0.1 (g)	400	98	54	25
Potential yield for 1990 year-class (t)	10.08	7.03	9.96	7.70

*F0.1 is a target fishing motality (Gulland and Boerema 1973).

Fig. 6. Average annual predation mortality rates by grey seals on the three length-classes of ESS cod under two assumptions about the instantaneous rate of residual natural mortality (M): (*a*) $M = M_C$ (constant) and (*b*) $M = M_{AS}$ (age specific). There is no estimate of the F on the smallest size-class for 1993 and 1994 because by convention 3 years is the youngest age fit in the VPA model for this cod stock.

thus the consumption of cod and other prey. Both cod and total food consumption were also insensitive to a change in the correction factor for prey that may not have been detected by the methods used to determine diet composition. Although we changed each parameter independently to isolate their effects, in reality they will often covary; for example, the percentage of cod may covary with the average energy density of the diet.

Effects of seal predation on cod

Predation by grey seals can be viewed as an analog to the catch from a fishery. In this section we compare the mortality of cod from predation by grey seals with that generated by the commercial fishery. The effect of the commercial fishery on the ESS cod population was assessed annually (Fanning et al. 1995) using virtual population analysis (VPA). The fishery data covered the period 1970–1994 and cod 1–15 years of age. Landings at age and survey numbers at age were fit to a population model using an NLLS procedure (Fanning et al. 1995). The landings at age were converted into cod numbers at age subject to assumptions about natural mortality (M). The rate of 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 from all sources, including grey seals, of ESS cod is

0.2 for all ages. When estimating the rate of seal predation mortality, assumptions about the magnitude and age-specific pattern of M become quite important.

There have been few attempts to measure age-specific M in cod. Some authors (Beverton and Holt 1959; Pauly 1980) inferred M from other biological characteristics such as life-span and growth rate. Sparholt (1990) and the ICES Working Group on Multispecies VPA investigated this issue in North Sea groundfish. This working group (Anonymous 1993) reported M values of 0.8, 0.35, and 0.25 for ages 1–3 and 0.2 for age 4 and older for North Sea cod on the basis of fish diets and a multispecies VPA. Because ESS cod grow more slowly 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) and in the absence of data on ESS cod, we assumed that M of juvenile ESS cod is higher and persists at high levels for 1 year longer than reported for North Sea cod. We used the following vector of M values: 1.0, 0.8, 0.6, and 0.4 for ages 1 to 4, respectively, and 0.2 for ages 5–15. To assess the impact of these two assumptions about other sources of M on estimates of seal predation mortality, we ran all analyses twice, once with $M = 0.2$ across all ages and again using the age-specific vector. Hereafter, we will denote the constant natural morality as M_C and the age-specific version as M_{AS}. Figures 6–12 compare results

Fig. 7. Instantaneous total (*Z*), fishing (*F*), and grey seal predation (M_S, under the constant ration model) mortality rates on ESS cod averaged over ages 2–7 with explicit grey seal predation in the VPA. (*a*) $M = M_C$ (constant) and (*b*) $M = M_{AS}$ (age specific).
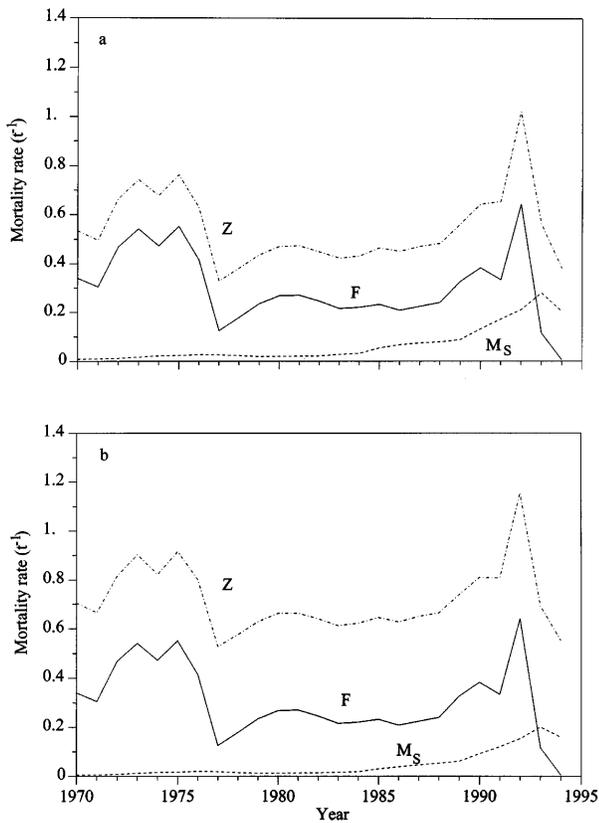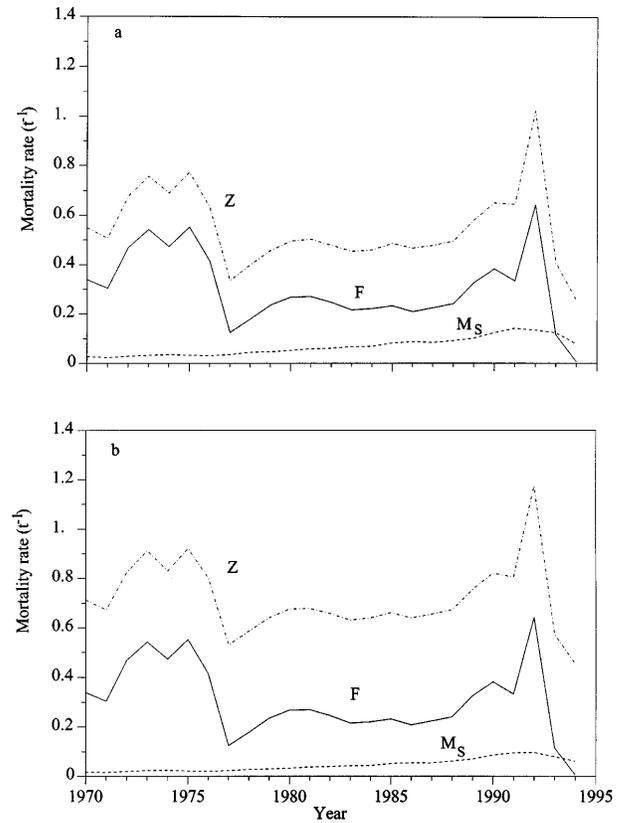

Fig. 8. Instantaneous total (*Z*), fishing (*F*), and grey seal predation (M_S, under the proportional ration model) mortality rates on ESS cod averaged over ages 2–7 with explicit grey seal predation in the VPA. (*a*) $M = M_C$ (constant) and (*b*) $M = M_{AS}$ (age specific).

under the two assumptions of cod natural mortality. Although we cannot be sure that they represent extremes, the comparison represents a wide range of possibilities.

Seal predation mortality

Grey seal predation mortality (M_S) of ESS cod was estimated by first running a standard VPA using the commercial landings and research trawl survey data as inputs and then performing the NLLS fit as described in Fanning et al. (1995). This resulted in estimates of age-specific population numbers and fishing mortalities of cod. The consumption of ESS cod by grey seals was then added to the commercial landings and the VPA was repeated. The VPA was then tuned again to account for the removals by grey seals. This combined cod mortality was then partitioned into deaths from the commercial fishery and those from grey seal predation. For this and the remainder of the analyses in this paper, we used both the constant and proportional ration models of grey seal consumption.

If seal predation mortality were additive, both cod recruitment at age 1 and population size would increase because the sum of M_S and M_R (i.e., residual M from sources other than seals) would be larger than M alone. However, at present we do not know how much compensation might occur among the components of M. Therefore, to allow more direct comparisons both 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 under the constant ration model. This meant reducing M to 85% of M_C and reducing M to 97% of M_{AS} before adding in the seal predation component of natural mortality, M_S. We did not follow this procedure in the estimation of yield per recruit to emphasize the potential contribution of additive seal predation mortality in each decade.

Under the assumption that $M = M_C$, the smallest length-class of cod consistently had the highest seal predation mortality rate, increasing rapidly in the early 1980s to about 0.58 in 1992 (Fig. 6*a*). The rate of seal predation mortality on larger cod was generally <0.05 until the late 1980s when mortality rose quickly as the cod stock declined. When M_{AS} 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 1980s (Fig. 6*b*). This result was expected, because predation by seals was now being compared with a higher residual natural mortality, which implies a larger cod population in the VPA. Nevertheless, even in this case, total mortality owing to seals was >0.2 by the late 1980s. Given that grey seals prey mainly on small cod, seal predation mortality on larger cod was largely unaffected by our assumptions about M (Fig. 6).

The mortality attributable to seal predation may be put into context by comparing it with both fishing and total mortality (Figs. 7 and 8). Mortalities owing to seals and owing to the fleet were averaged over ages 2–7. The reduction in total mortality

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Fig. 9. VPA estimates of age-1 recruitment in ESS cod for 1970–1992 with (solid line) and without (dotted line) explicit seal predation using the constant ration model. Projected mean recruitment and 95% confidence limits for the period 1993–1995 are indicated by the solid-line series (see text for details). The dashed-line series are the model predictions of recruitment after grey seal predation had occurred. (*a*) $M = M_C$ (constant) and (*b*) $M = M_{AS}$ (age specific).

Fig. 10. VPA estimates of age-1 recruitment in ESS cod for 1970–1992 with (solid line) and without (dotted line) explicit seal predation using the proportional ration model. Projected mean recruitment and 95% confidence limits for 1993–1995 are indicated by the solid-line series (see text for details). The dashed-line series are the model predictions of recruitment after grey seal predation had occurred. (*a*) $M = M_C$ (constant) and (*b*) $M = M_{AS}$ (age specific).
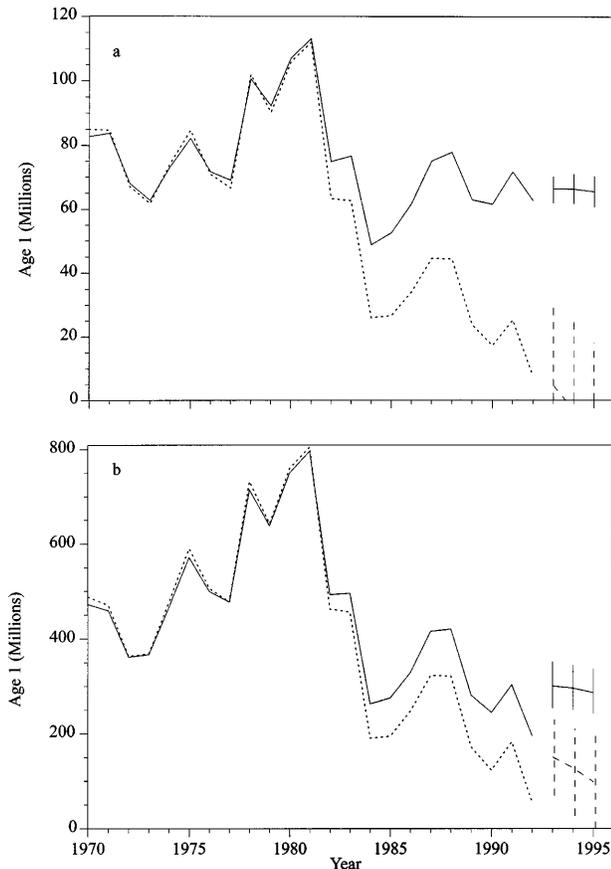
of ESS cod seen in the late 1970s was due to the nearly total exclusion of foreign fishing effort in 4Vs and 4W with the extension of Canadian jurisdiction to 200 miles. In the constant ration model (Figs. 7*a* and 7*b*), under either assumption about residual *M*, the contribution by grey seals to total mortality was small until the late 1980s but became more pronounced in the 1990s as the number of grey seals continued to increase while the cod population rapidly decreased in size. Interestingly, seal predation mortality on the 2- to 7-year-old cod levelled off in 1994, despite a continued increase in the number of grey seals. This was probably caused by the presence of the 1990 year-class, which was large compared with adjacent year-classes. Under the proportional ration model (Figs. 8*a* and 8*b*), grey seal predation mortality increases slowly throughout most of the period, but is still low compared with fishing mortality.

Recruitment

We examined the potential impact of grey seal predation on estimates of recruitment (i.e., numbers at age 1) in the population by running the VPA without and with explicit seal predation. The dotted line in Figs. 9 and 10 from 1970–1992
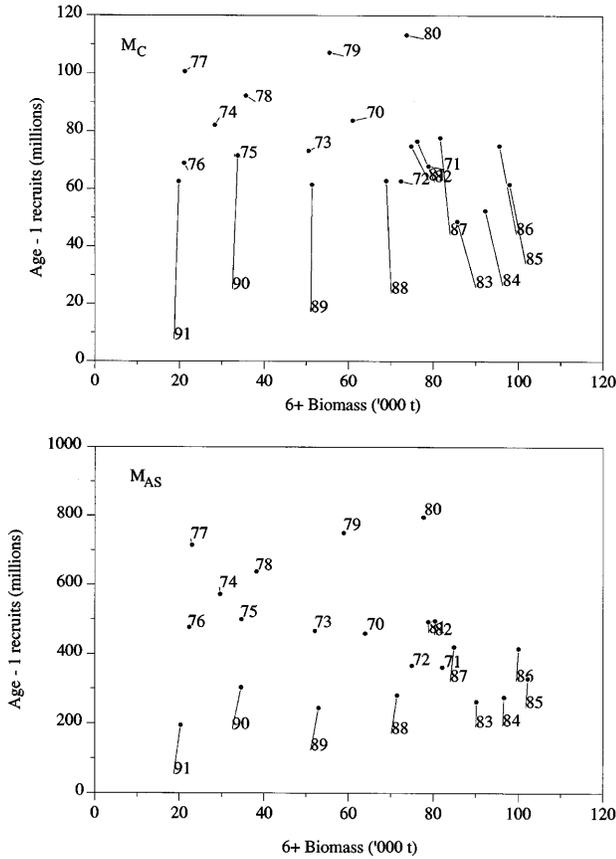
represents the estimated recruitment from the VPA when grey seal predation is not explicitly included in the model assumptions about *M*. In this standard version of the VPA (e.g., Fanning et al. 1995), recruitment estimates of ESS cod declined rapidly during the 1980s and early 1990s (Figs. 9 and 10). However, when seal predation was explicitly added to this model (i.e., accounting in the VPA for the age-1 cod estimated to have been eaten by grey seals) recruitment at age 1 appeared not to have been so severely reduced during this recent period, although the effect was less in the proportional ration model (Fig. 10*a*). Under the assumption of M_{AS}, in both the constant (Fig. 9*b*) and the proportional (Fig. 10*b*) models, the effect of grey seal predation on apparent recruitment was reduced because the predation took place on a population in which the number of recruits was about 6 times greater owing to the higher mortality at young ages.

Stock-recruitment relationship

The addition of explicit seal mortality to the VPA also affected the stock-recruitment pattern of ESS cod (Fig. 11). In interpreting Fig. 11, it is important to remember that the underlying assumption in the model is that seal predation is additive and
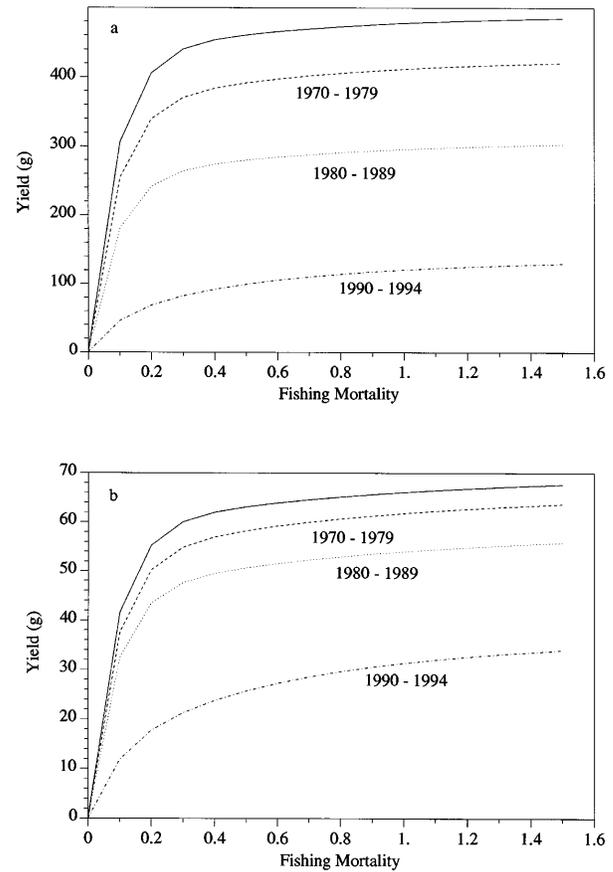
Fig. 11. Stock-recruitment relationships with (solid dots) and without (numerals) grey seal predation added to the ESS cod VPA. For each year, the number locates the parent stock and corresponding recruitment in the absence of explicit seal predation. This number is joined by a line to a dot, which is the same year's position after including predation by grey seals. The underlying assumption in the model is that seal predation is additive. (*a*) $M = M_C$ (constant) and (*b*) $M = M_{AS}$ (age specific).

Fig. 12. Yield per recruit of ESS cod without grey seal predation (solid line) and incorporating grey seal predation mortality for 1970–1979, 1980–1989, and 1990–1994. (*a*) $M = M_C$ (constant) and (*b*) $M = M_{AS}$ (age specific).

independent of cod abundance. If there were strong compensation in the components of M, then the effect of predation on the estimated stock and recruitment would be less (i.e., the length of the lines shown in these figures would be shorter). Thus, the end points of each line are the extremes of the degree of compensation for seal mortality in the predator field.

The lines are too short to be visible for the early years, but under either assumption about M, the lines increase in length over time. Without explicit seal predation, recruitment fell significantly through the 1980s despite a high biomass of spawners and continued to fall at moderate spawning stock size in the late 1980s. Adjusting for the effects of grey seal predation substantially increased the initial size of the 1983–1990 year-classes. When $M = M_C$ 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 M_{AS} was assumed. However, in neither case did seal predation account for the decrease in year-class size during much of the 1980s compared with that observed during the 1970s, suggesting an increase in other sources of natural mortality or reduced spawning success.

Yield per recruit

The potential impact of grey seal predation on the yield of ESS cod was examined through a yield per recruit analysis (Thompson and Bell 1934). The yield per recruit model balances cod growth with removals and deaths at age. Yield per recruit of cod may have been reduced by >50% as a result of seal predation in the most recent period (Figs. 12*a* and 12*b*), provided that seal predation mortality was additive. Note that the magnitude of the yield varied by 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 ESS cod cannot currently 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. Again, the dotted curves in Fig. 12 are based on the assumption that grey seal M_S is additive. 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 would have had no effect on yield per recruit. Clearly, neither of these extremes is likely and thus the effect

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of grey seals on yield per recruit of cod will probably fall between the dotted curves and the solid curve in Figs. 12a and 12b.

The implications of the yield per recruit calculations are best evaluated in the context of the effect that explicit seal predation mortality has on levels of recruitment. This is because the reduction in the yield per recruit is partially compensated for by an increase in the level of recruitment implied by seal predation (see Figs. 9 and 10) and the potential yield from a year-class is the product of the yield per recruit and the size of a year-class. For example, under the assumption of $M = M_C$, the estimate of the 1990 year-class more than doubles when seal predation is included in the model, whereas the yield per recruit decreases to approximately 25% (Table 1). The net effect is about a 30% loss in potential yield from this year-class. Implicit in this calculation is that fishing, seal predation, and residual natural mortality patterns remain constant over the period that this year-class would have been in the fishery (i.e., until about the year 2000). Similar results are obtained under the assumption of M_{AS}.

Potential effect of greyseals on future recruitment

To examine the impact of grey seal predation on future cod recruitment, we compared estimates of recruitment from VPA models that explicitly included seal predation, such that $M = M_R + M_S$, with models in which seal predation is an unspecified part of M. For example, in the standard VPA (Fanning et al. 1995), $M = 0.2$ includes seal and all other sources of natural mortality (e.g., dotted line in Fig. 9a). To determine the projected recruitment in 1993–1995 that would have occurred if seal predation had not, we bootstrapped the age-1 recruitment estimates from the VPA in which seal predation is modelled explicitly for the period 1982–1992. Confidence limits on the projected recruitment were based on 500 bootstrap replicates. Four projected recruitment series were generated using the two assumptions about M_R (i.e., M_C and M_{AS}), which affect the size of the estimated cod population, and the two ration models. An exponential weighting function with a time constant of 0.2 was applied to the recruitment estimates so that drawing the estimate from 1992 was about 7 times more probable than drawing the estimate from 1982. This form of projection was chosen because of the lack of a clear stock-recruit relationship and the reduced recruitment levels experienced by this stock in recent years. In each panel of Figs. 9 and 10, the upper series of projected recruitments for 1993–1995 are model estimates of the number of age-1 cod that are predicted to recruit to the population when the number of cod eaten by grey seals is accounted for explicitly in the VPA.

Grey seal population numbers and cod consumption were projected to 1995 using the population parameters in Table 1. A predictive relationship between the removals by seals each year and the difference between the two recruitment series (i.e., with and without explicit seals) was derived to estimate future differences between the two recruitment series given an estimate of grey seal consumption in each year. This was done by fitting a linear regression between these two variables for the period 1982–1992 for each of the four recruitment scenarios above. The model fit the data well; all regressions were significant at $p < 0.001$. The predicted differences in recruitment were then subtracted from our projected recruitment to predict the "realized" recruitments for 1993–1995 after explicit grey seal predation had occurred. These realized recruitments (the

dotted lines in Figs. 9 and 10) may be compared with the trend in recruitment from the standard VPAs (i.e., where seal predation is implicit). Because the lower series of projections has uncertainty owing to both the recruitment model and the predation model, its error bars are larger than those of the upper series, which include only the cod recruitment uncertainty.

The magnitude of the difference between the projected level of recruitment and that realized after seal predation depends both on our assumptions about the magnitude of residual mortality and on the form of the ration model (Figs. 9 and 10). In the constant ration model, future cod recruitment is significantly reduced by grey seal predation under either assumption about residual M (Figs. 9a and 9b). In fact, the most extreme prediction is that recruitment would fall to near zero (Fig. 9a) following the trend that is seen in the standard (i.e., implicit seal predation) VPA. The effect of grey seal predation is less in the proportional ration model. This is not surprising because in the proportional model grey seals eat fewer cod as cod become less abundant, but even here the model predicts significantly fewer recruits in the face of seal predation if $M = M_C$ (Fig. 10a). Only in the case of $M = M_{AS}$ did the model predict no significant reduction in cod recruitment by grey seal predation (Fig. 10b).

Discussion

Our analyses, indeed ecological models in general, may be viewed as a serial process that builds on each previous step by adding some new information to form the next; the number of seal pups plus vital parameters is used to estimate the number of grey seals, the number of seals plus their ration leads to estimates of cod consumption, a comparison of this consumption to the size of the cod stock leads to estimates of predation mortality, and finally the predation mortality plus a cod recruitment model leads to an estimate of impact. In the initial stages of this process (for example, the grey seal population models) there are often sufficient data to use bootstrapping to examine the uncertainty of the results. We realize that there are other sources of error for which data do not exist and thus our error bars must be viewed as minima. In the later steps of the analysis, uncertainty is dominated by model assumptions and we have used alternative models to explore the consequences of this uncertainty.

The grey seal population in eastern Canada has increased substantially over the past several decades and there can be little doubt that the number of grey seals inhabiting the study area has also increased. There is greater uncertainty in this latter statement because grey seals are capable of large-scale seasonal movements and our knowledge of these movements is scanty at present. The simple bioenergetic model used to determine grey seal food requirements produced estimates of the daily energy requirements of an average grey seal (7560 kcal/day) that are 29% higher than those in grey seals in the United Kingdom (5860 kcal/day) that were derived from a more complex energetic model (Fedak and Hiby in Anonymous 1984). Much of this difference is accounted for by the larger size of Canadian grey seals (Murie and Lavigne 1992) and by differences in the age structure of the modelled British and Canadian populations. Although additional data on the loss of ingested energy in urine, faeces, and heat would result in modest revision of our estimates, significant improvement

Fig. 13. A hypothetical space defined by the principal assumptions in the predation model. The ellipsoid depicts our subjectively defined region for the likely domain of the grey seal – ESS cod model.
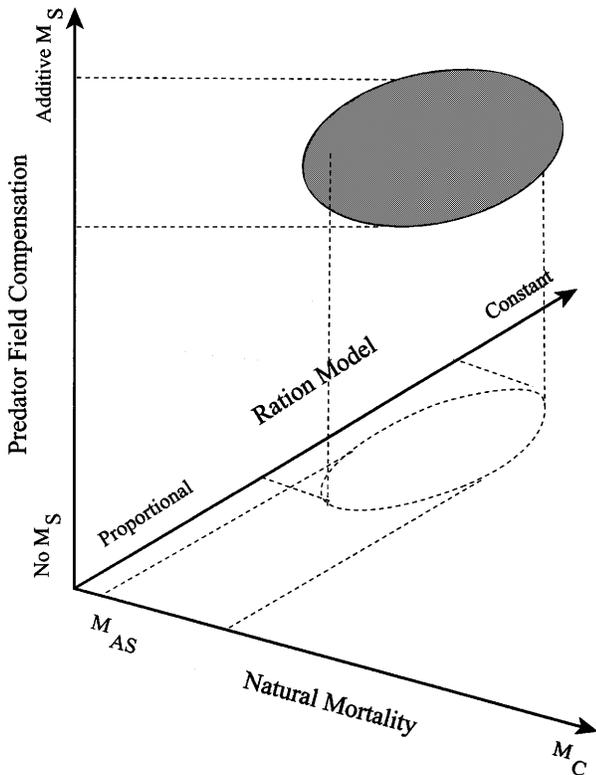
in the model precision must await better estimates of the ADMR of grey seals.

The significance of these consumption estimates is more meaningful when they are expressed as mortality rates. A comparison of the relative magnitudes of mortality caused by fishing and grey seals provides an assessment of their relative contributions to the recently observed decline in ESS cod abundance. Under the constant ration model with residual $M = M_C$, M_S averaged about 16% of fishing mortality over the period 1970–1992, and about 11%, for the same period, under the assumption of residual $M = M_{AS}$. Similarly for the proportional ration model, the fractions were about 20 and 13%, respectively, for the two assumptions about residual M. As fishing mortality is based on reported landings rather than the actual catch from the stock, fishing mortality may have been even higher than reported here. Thus, the model results show that grey seals played a relatively minor role in the recent collapse of this fishery. This conclusion is robust to model uncertainties.

However, the larger and perhaps increasing predation mortalities seen in the 1990s raise the possibility that grey seal predation could inhibit the recovery of the ESS cod and reduce the yield from future fisheries. How likely is this possibility? The answer seems to depend very much on what we know about the magnitude of other components of M on cod, the functional form of grey seal predation, and the extent to which seal predation mortality on cod is additive. Figure 13 is a three-dimensional representation of these three principal uncertainties.

To assess the importance of these uncertainties on our conclusions, we have attempted to span this hypothetical space by assuming extremes. For example, in the case of the functional form of predation, we assume that the fraction of cod in the diet is either constant (i.e., independent of cod abundance) or directly proportional to cod abundance. The axes in Fig. 13 have been arranged such that the impact is decreased as the origin is approached. Although the axes are displayed as being orthogonal, there would be a strong interdependence among them. The ellipsoid depicts our subjectively defined region for the likely domain of the grey seal – ESS cod model.

There seems to be broad agreement that the M of juvenile fish is greater than that of adults (e.g., Sparholt 1990), but less agreement or data on actual age-specific estimates for Atlantic cod. Nevertheless, it seems clear that the usual assumption of $M = 0.2$ for all ages is unlikely to hold and that estimates of seal predation mortality on ESS cod are more likely to approach those calculated under our assumption that $M = M_{AS}$. The number of cod recruits estimated from the model is very sensitive to the assumed background level of M. This in turn has a great effect on the level of mortality associated with grey seal consumption of cod and the potential impact of this predation mortality.

The amount of ESS cod eaten by grey seals depends heavily on the form of the predation model. Given the dramatic drop in the abundance of ESS cod, the proportional model predicts that grey seals would consume considerably less cod (about 4000 – 10 000 t) in 1994 than under the constant ration model (about 10 000 – 22 000 t). The proportional model also predicts little difference in short-term projections of recruitment between the model with or without explicit grey seal predation. We do not know which type of functional response best describes grey seal predation. Three types of functional responses were proposed by Holling (1959). They all increase from the origin and have an asymptotic nature. We have proposed two simpler models of functional response. The constant ration model may be thought of as type 0, as it has no slope, whereas the proportional ration model is like a type 1 except that no plateau is defined, although logically it must exist. These simpler forms were used because existing data were insufficient to fit the more complicated forms and because they represent a broad range of predator functional response.

By analogy with other vertebrate predators, there are theoretical reasons for expecting that grey seals may exhibit a type 2 or 3 functional response (Holling 1959; Peterman and Gatto 1978; Murdock and Oaten 1975; Hilden 1988). A type 2 functional response appears to be characteristic of fish faced with a single prey, but prey switching results in type 3 responses (reviewed in Murdock and Bence 1987). The type 2 response is common in invertebrates and small mammals (Taylor 1984). Empirical studies suggest that it will be difficult to distinguish type 2 and type 3 functional responses in field data of the type that will be possible to gather for grey seals and other marine mammals. Yet these two responses can produce quite different system behaviour with respect to the impact of predation on prey populations (Peterman and Gatto 1978; Hilden 1988): a type 3 response is stabilizing whereas a type 2 response is destabilizing and is thought to be the reason why freshwater predators are often capable of eliminating prey populations (reviewed in Murdock and Bence 1987). Clearly, more research is needed on large mammalian predators.

Recent studies (Bowen et al. 1993; Bowen and Harrison 1994) indicate that northern sand lance (*Ammodytes dubius*) is the dominant prey offshore and that pelagic species such as herring account for most of the inshore diet. Thus, grey seal population size and predation pressure may be only weakly coupled with the abundance of ESS cod such that grey seals may continue to prey on cod even when the abundance of cod is low. It is this possibility of a depensatory mechanism that could affect the magnitude and timing of the recovery of ESS cod.

We have only examined one model of the interaction between seals and ESS cod, a simple grey seal – fishery – cod model. Harwood (1983) and Beverton (1985) discuss a number of more complex models for the interactions between seals, fisheries, and prey populations that should be considered in future work. The concept of a minimum realistic model has recently emerged from modelling studies of the interactions among Cape fur seals (*Arctocephalus pusillus pusillus*), commercial fisheries, and fish species in the Benguela current (Anonymous 1991; Butterworth 1992). The concept is that attempts to evaluate the impact of seal predation on commercial fish stocks should be based on multispecies models that account for the more important species and their interactions. Clearly, the challenge is to know what to include (i.e., what is important) from potential data sources.

The grey seal – fishery – ESS cod model we have developed falls short of what is likely to be a minimum realistic model for the ESS study area. Our lack of knowledge about other predators of cod and the abundance and dynamics of other prey, especially sand lance, prohibits the development of more detailed models at this time. Young cod are eaten by fish predators on the ESS and adjacent areas (Kohler and Fitzgerald 1969; Langton and Bowman 1980), but there are no current data on the extent of this predation. In other marine ecosystems, fish predators are the major source of *M* (e.g., Overholtz et al. 1991; Bax 1991; Livingston 1993), particularly on young of the year fish. Thus, the magnitude of fish predation on ESS cod needs to be determined.

The impact of seal predation mortality on the dynamics of cod also depends heavily on the extent to which seal mortality is additive or is compensated for by a decrease in other sources of natural mortality. Additivity is a basic assumption of multispecies virtual population models (Sparholt 1990). However, little is known about how the components of natural mortality respond to changes in predator abundance.

Despite the difficulties and uncertainties associated with producing estimates of consumption by seals, as our results underscore, such estimates are only the first step toward an understanding of the impact of seal predation on prey population dynamics. In the context of fisheries management, estimates of consumption are of relatively little value unless they can be expressed in terms of a mortality rate. This increases uncertainty because of the imprecise nature of estimates of the size- or age-specific abundance of fish populations. Further uncertainty about the impact of seal predation mortality on the dynamics of prey populations arises because we do not know the functional relationships among or the magnitude of the other components of natural mortality. Thus, we are faced with increasing levels of uncertainty as we move from calculations of population food consumption, to estimates of predation mortality, and finally to estimates of the effect of this seal predation mortality on the dynamics of prey populations. Although important questions remain to be answered with respect to the seal predation (for example, bias in diet composition, at-sea distribution, and functional response to prey density), some of the greatest sources of uncertainty can be traced to our lack of knowledge about the age-specific pattern of natural mortality on young cod, the interactions among sources of natural mortality on cod, and the abundance and dynamics of forage fish populations such as sand lance that are shared prey of both grey seals and Atlantic cod.

Acknowledgments

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