

CONTINUED DECLINE OF AN ATLANTIC COD POPULATION: HOW IMPORTANT IS GRAY SEAL PREDATION?

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Abstract. The continental shelf ecosystem on the Eastern Scotian Shelf (ESS) has experienced drastic changes. Once common top predators are a small fraction of their historical abundance, and much of the current community structure is now dominated by pelagic fishes and invertebrates. Embedded within this food web, Atlantic cod and gray seal populations have recently exhibited nearly opposite trends. Since 1984, cod populations have decreased exponentially at a rate averaging 17% per year, whereas gray seals have continued to increase exponentially at a rate of 12%. We reexamined the impact of gray seals on Atlantic cod dynamics using more than 30 years of data on the population trends of cod and gray seals while incorporating new information on seal diet and seasonal distribution. The closure of the cod fishery over 10 years ago allowed for a better estimation of natural mortality rates. We quantified the impact of seals on ESS cod by (1) estimating trends in seal and cod abundance, (2) estimating the total energy needed for seal growth and maintenance from an energetics model, (3) using estimates of the percentage of cod in the total diet derived from quantitative fatty acid signature analysis (QFASA) and of the size-specific selectivity of cod consumed (derived from otoliths collected from fecal samples), and (4) assuming a gray seal functional response. Uncertainties of the model estimates were calculated using the Hessian approximation of the variance–covariance matrix. Between 1993 and 2000, cod comprised, on average, <5% of a gray seal's diet. Our model shows that, since the closure of the fishery, gray seals have imposed a significant level of instantaneous mortality (0.21), and along with other unknown sources of natural mortality (0.62), are contributing to the failure of this cod stock to recover.

Key words: Atlantic cod; energetics model; *Gadus morhua*; generalist predator; gray seal; *Halichoerus grypus*; population dynamics model; population recovery.

INTRODUCTION

Changes that are unprecedented during the past several centuries have occurred recently in the world's oceans, including marked declines in top predators. Sharks (Baum et al. 2003, Baum and Myers 2004), tuna and billfish (Cox et al. 2002, Myers and Worm 2003, Ward and Myers 2005), and some whales (Clapham et al. 1999) are currently a small fraction of their historical abundance. These decreases, along with the concurrent increases in pelagic fishes (Fogarty and Murawski 1998) and invertebrates (Worm and Myers 2003), may indicate that vast regions of the ocean have entered a new dynamical regime (Zwanenburg et al. 2002, Choi et al. 2004, Frank et al. 2005, Mangel and Levin 2005, Myers and Worm 2005).

Atlantic cod (*Gadus morhua*) populations have also been decimated throughout their range, primarily due to overfishing (Hutchings and Myers 1994, Myers et al.

1996, 1997a). Many fisheries managers and scientists expected cod to recover quickly after fishing moratoria were imposed on stocks off eastern Canada in 1992 and 1993. This view was based on the assumption that cod were resilient to large decreases in abundance because of their high fecundity. Furthermore, several cod populations, including that on the Eastern Scotian Shelf (ESS), rapidly recovered when fishing pressure was reduced in 1977 with the introduction of the 200-mile limit, which extended Canada's fishing jurisdiction and had the effect of reducing fishing pressure from foreign fleets. However, Canada's fishing fleet rapidly filled this gap. Few ventured to predict recovery times after the moratoria; however, Myers et al. (1997b) used a Ricker model to predict an 18% population increase under the best of conditions, or a doubling time of four years, with a fishable population in a little over 10 years. Nevertheless, cod and many other depleted fish stocks have not recovered (Hutchings 2000, Hutchings and Reynolds 2004). Dangerously low levels of cod abundance have prompted the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) to recommend that the Canadian government list the cod populations of Newfoundland and Labrador as endangered, the population of the northern Gulf of St. Lawrence as

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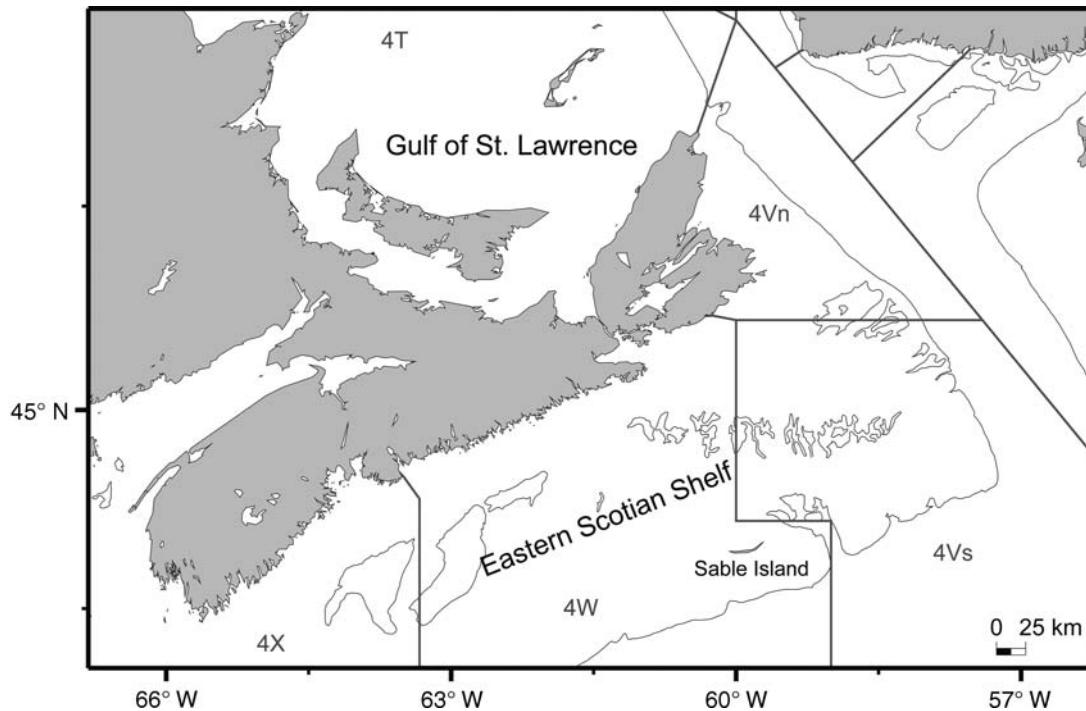


FIG. 1. Eastern Scotian Shelf (NAFO [Northwest Atlantic Fisheries Organization] subareas 4W and 4Vs) and southern Gulf of St. Lawrence (NAFO subarea 4T), Canada.

threatened, and the Maritime population as of special concern (COSEWIC 2003). The failure of those stocks to recover may be due, in part, to low reproductive rates at low population size (Myers et al. 1999), but a lack of a broader understanding of how population growth rate is affected by the environment (Brander and Mohn 2004), fish behavior (Brawn 1961, Rowe and Hutchings 2003), and food-web interactions (Yodzis 1998, 2000) may also be involved.

The potential negative effects of upper-trophic-level predators, such as pinnipeds, on the dynamics of fish populations of commercial importance has been hypothesized for decades (e.g., Malouf 1986) and is a continuing source of debate among fishermen, resource managers, and ecologists (FRCC 2001, Lavigne 2003). However, concern about the effect of pinniped predation on prey populations is simply an example of the broader issue of the role of top-down effects on prey dynamics and the structure and functioning of marine ecosystems worldwide (e.g., Estes et al. 1998, Myers and Worm 2005).

The ESS cod stock, located off the coast of Nova Scotia, Canada (Fig. 1, Northwest Atlantic Fisheries Organization [NAFO] subdivisions 4Vs and 4W), has been fished for several centuries (Rosenberg et al. 2003). From 1958–1974, commercial landings of this stock ranged between 40 000 and 80 000 t (1 t = 1 Mg) before declining to 10 000 t in 1977 (Fanning et al. 2003). The stock increased after the establishment of the 200-mile limit in 1977, and landings peaked at 50 000 t in 1985.

Since 1984, cod abundance has declined exponentially at a rate of 17% per year, and in 1993, a fishing moratorium was imposed and remains in effect. The mass of age-8 cod peaked in the late 1970s then decreased monotonically from 5.5 kg to 2.0 kg; during this same period, age at maturity decreased from age four to three (Fanning et al. 2003). ESS cod used to spawn in both the spring and fall, but now only the fall spawning component remains (Frank et al. 1994).

In contrast to the widespread declines of many marine predators, gray seal (*Halichoerus grypus*) populations have increased in eastern Canada. Most gray seals are born at colonies located in the southern Gulf of St. Lawrence and on Sable Island located on the Eastern Scotian Shelf, but newer and smaller colonies are located along the eastern shore of Nova Scotia and at several sites in the northeastern United States (Mansfield and Beck 1977, Hammill et al. 1998, Waring et al. 2002). Gray seals are large (adults weigh between 100 and 350 kg), wide-ranging predators that exhibit marked seasonal changes in distribution and foraging effort (Beck et al. 2003b, Austin et al. 2004; G. Breed et al., unpublished manuscript). They are generalists, feeding on a wide range of pelagic and demersal fishes, including Atlantic cod (Bowen et al. 1993, Bowen and Harrison 1994). The population breeding on Sable Island is a striking example of the exponential increase of a long-living marine mammal, having increased at a rate of 12.8% annually for more than 25 years (Bowen et al. 2003). An earlier study found that gray seals had little

effect on the collapse of cod on the ESS (Mohn and Bowen 1996); however, a more recent study suggested that gray seal predation was impeding population recovery (Fu et al. 2001).

Understanding the factors, including predation, that limit the recovery of depressed populations is clearly important to design effective recovery strategies (Sinclair et al. 1998). Even if the limiting factors are beyond our control (e.g., ocean temperature), a better understanding of the limiting factors provides a firmer basis for establishing expectations about both the timeframe and extent of recovery. The closure of the cod fishery in 1993, more than 30 years of data on the population trends of cod and gray seals, new information on gray seal diet, derived from quantitative fatty acid signature analysis (QFASA), and seasonal distribution data of gray seals derived from satellite tags, provide a basis for reexamining the impact of gray seals on the dynamics of a severely depressed stock of Atlantic cod. We used a statistical catch-at-age population model of ESS cod and compared estimated gray seal predation mortality to other sources of mortality.

METHODS

We quantified the impact of gray seals (*Halichoerus grypus*) on Eastern Scotian Shelf (ESS) Atlantic cod (*Gadus morhua*) by (1) estimating trends in seal and cod abundance, (2) estimating the total energy needed for seal growth and maintenance using an energetic model, (3) using estimates of the percentage of cod in the total diet and the size-specific selectivity of cod consumed, and (4) modeling a gray seal functional response. The model was constructed using AD Model Builder (Fournier 1996). Maunder (2004) provides a succinct review of the structure and capabilities of AD Model Builder. The model first fit to seal and cod abundances, then estimated the number of cod consumed based on seal diet information and the energy needed to maintain estimated gray seal population trends.

Uncertainties in terms of variances for model parameters and state variables were estimated from the Hessian approximation of the variance-covariance matrix at the optimized solution. A Bayesian model with informative priors and resultant posteriors was not performed because the data would not support the estimation of the variances in the likelihood function. Instead, these variances were assumed or inferred from the literature. Thus, for most parameters, means and variances were used as penalty functions (Appendix) in a role similar to Bayesian priors. Some parameters were fit in log space to avoid negative values (like numbers at-age) and because the log data had better behaved error distributions.

Estimating gray seal abundance

As in Mohn and Bowen (1996), we separately estimated population trends on Sable Island and other Canadian colonies, including the Gulf of St. Lawrence.

The pup production of gray seals on Sable Island was estimated in most years from 1962 to 1990 based on tagging all weaned pups (Mansfield and Beck 1977, Stobo and Zwanenburg 1990). High population abundance in recent years required that pup production be estimated from aerial photography (Bowen et al. 2003), with the most recent estimate being in the spring of 2004 (Bowen et al., *in press*). Both year-class tagging and aerial surveys were conducted on Sable Island in 1989 and 1990 and indicated that the two methods gave comparable results (Bowen et al. 2003). Pup production in the Gulf of St. Lawrence was estimated from mark-recapture studies (Hammill et al. 1992, 1998, Myers et al. 1997a) and aerial surveys (Hammill and Gosselin 2005). Estimates of pup production in the Gulf of St. Lawrence are more variable than at Sable Island because pups are born on drifting ice, suffer higher mortality, and are more difficult to census (Myers et al. 1997a, Hammill et al. 1998). Production at small islands in the Gulf of St. Lawrence and along the eastern shore of Nova Scotia was determined by visual counts or year-class tagging.

Previously, a simple exponential population model was fit to the data on pup production (Mohn and Bowen 1996, Bowen et al. 2003), however, the Sable Island population has begun to show evidence of density dependence. Females were about 16 times less likely to be primiparous at-age 4 yr from 1998 to 2000 compared to cohorts in the mid to late 1980s, and the upper 95% confidence interval for pup production in 2004 falls below confidence intervals predicted from the exponential model (Bowen et al., *in press*). Consequently, we parameterized a theta-logistic model using several assumptions about the strength and timing of density dependence and the level of carrying capacity.

We denoted the total number of seals as $N_{t,a,s}$, where the subscript t indexes the year; a , age; and s , sex. In our model, age-0 refers to pups in their first year of life (from birth to January 1st the following year). Males ages 1–9 yr and females ages 1–5 yr were considered as juveniles, even though some females can give birth as early as age 4. Males older than 9 yr and females older than 5 yr were referred to as adults. We distinguished between mortality at different life stages using superscripts (e.g., M^{Pup} or M_f^{Adult}), and use subscripts to denote rates for different sex or age classes.

Reviews of population dynamics in large mammals indicate that one of the first signs of density dependence is a decrease in juvenile survival (Fowler 1987). It is at this stage that we model density dependence in the Sable Island population with the theta-logistic function. We assumed that all other natural mortality rates were instantaneous, density independent, and constant over our study period. Given the observed exponential rate of increase of pup production in the Sable Island population over the period from 1976 to 1997, these assumptions seem warranted (Bowen et al. 2003) but will need to be modified as the population approaches

carrying capacity. Data on pup production suggest that mortality rates in the Gulf of St. Lawrence population are not constant, but this assumption is necessary to approximate population dynamics with the exponential model. For both the Sable Island and Gulf of St. Lawrence populations, we used separate mortality rates for pups, juveniles, and adults. The age-specific birth rates b_a , were based on pregnancy rates reported in Mansfield and Beck (1977) and Hammill and Gosselin (1995). We used a 1:1 sex ratio at birth (Bowen, unpublished data).

The number of pups produced in the next year, $P_{t+1,s}$, is the sum of the number of females, $N_{t,a,f}$, multiplied by the age-specific pregnancy rate b_a :

$$P_{t+1,s} = 0.5 \left(\sum_a N_{t,a,f} b_a \right). \tag{1}$$

The number of pups surviving to the next year in the Sable Island population is given by

$$J_{t+1,1,s} = P_{t,s} e^{-M^{Pup}} \left[1 - \left(\frac{N_t}{K} \right)^\theta \right] \tag{2}$$

where N is total population size, K is carrying capacity, and θ is the degree of density dependence. The degree of density dependence in gray seals is unknown, but Harting (2002:101) argued that θ for marine mammals should be around 2.4, which he found support for in monk (*Monachus schauinslandi*) and fur seals (Taylor and DeMaster 1993). We use this value, 2.4, in our analysis. The number of juveniles (juvenile males ages 1–9, females ages 1–5 yr) in the Sable Island population is given by

$$J_{t+1,a,s} = J_{t,a,s} e^{-M^{Juv}} \left[1 - \left(\frac{N_t}{K} \right)^\theta \right]. \tag{3}$$

Since carrying capacity can not be estimated without more data, we varied K until the 2004 model estimate of pup production fell within the confidence interval of the 2004 aerial survey estimate. M^{Pup} was estimated from the pup count data, whereas M^{Juv} was fixed (Table 1). Our model did not allow adults to survive beyond age 39. Adult numbers (males aged >9, females aged >5) are given by

$$A_{t+1,a+1,s} = \left(\frac{J_{t,a,s} e^{-M^{Juv}}}{A_{t,a,s} e^{-M_s^{Adult}}} \right). \tag{4}$$

Total population size is given by

$$N_t = \sum_{a,s} P_{t,s} + \sum_{a,s} J_{t,a,s} + \sum_{a,s} A_{t,a,s}. \tag{5}$$

The model for the Gulf population assumed density-independent survival for all stages and accounted for hunting removals (Zwanenburg and Bowen 1990, Hammill et al. 1998). Mohn and Bowen (1996) argued that mortality rates should be different for males and females

TABLE 1. Instantaneous rates of natural mortality (mean \pm SE) for Sable Island and Gulf of St. Lawrence gray seal populations.

Parameter	Instantaneous rate of natural mortality	
	Sable Island	Gulf of St. Lawrence
M^{Pup}	0.103 \pm 0.044	1.46 \pm 0.089
M^{Juv}	0.0507 \pm 0.005	0.0507 \pm 0.005
M^{Adult}_{male}	0.0507 \pm 0.005	0.0507 \pm 0.005
M^{Adult}_{female}	0.0506 \pm 0.005	0.0503 \pm 0.005

Notes: Initial population size and pup mortality (in 1962) were estimated by fitting to pup count data. Initial population (N_{1962}) was 392 \pm 25 seals for Sable Island and 3704 \pm 372 for Gulf of St. Lawrence (mean \pm SE). Mortalities for juveniles and for adult males and females were set at 0.05, and the uncertainty was modeled by a lognormal distribution with $\sigma = 0.1$ (see *Methods: Estimating gray seal abundance*).

based on their differences in longevity; however, there are few data that can be used to evaluate this assumption. Consequently, we fixed the mortality rates of juveniles, adult males, and adult females at the values guided by Mohn and Bowen (1996), Schwarz and Stobo (2000), Hall et al. (2002), and Manske et al. (2002). (Although instantaneous rates of mortality or predation are formally defined in units of reciprocal time (years), for readability they have been dropped.) Schwarz and Stobo (2000) noted that their estimates of adult female survival (0.92) was probably biased low, while Manske et al. (2002) indicated that their estimate of adult male survival (0.97) was probably biased high. We split the difference and assumed that adult survival for male and females was 0.95, which corresponds to an instantaneous mortality of 0.05. We modeled the uncertainty in these parameters with a lognormal distribution where $\sigma = 0.1$. Juveniles were assumed to have the same mortality as adults (Table 1). The rates concur with observations that males and females often live to their mid 30s, while a few survive into their early 40s. Estimates of pup mortality were obtained by minimizing an objective function that is the sum of the negative-log likelihoods for the pup count data from both populations (Quinn and Deriso 1999). We used lognormal error structures for all likelihoods.

We incremented our predator-prey model on a quarterly basis. For pups, the annual mortality was partitioned such that 75% occurred between January and July, whereas survival was assumed to be constant over the season for juveniles and adults.

Juvenile and adult gray seals move long distances during foraging, and mark-recapture data indicate there is some movement between the Sable Island and Gulf of St. Lawrence breeding populations (Mansfield and Beck 1977, Stobo et al. 1990, Lavigne and Hammill 1993). We updated assumptions about seasonal movement in Mohn and Bowen (1996) with data on at-sea distribution of gray seals derived from Argos based satellite tags. Tags were fitted to juvenile and adult gray seals in the southern Gulf of St. Lawrence in the summers of 1993–

TABLE 2. The percentage of the Sable Island and Gulf of St. Lawrence gray seal populations inhabiting the Eastern Scotian Shelf (ESS).

Population	Category	Seal population at ESS (%), by quarter			
		First	Second	Third	Fourth
Sable	YOY	92	97	83	93
	Male	66	81	64	75
	Female	87	76	60	74
Gulf	All	39	29	1	8

Notes: The Sable Island estimates are separated into three categories: young of the year (YOY) and males and females >1 year old ($n = 24, 49,$ and 51 individuals, respectively). The Gulf population estimates are for combined ages ($n = 54$ individuals). Estimates were derived from Argos-based satellite tags.

2004 (M. Hammill, *unpublished data*) and at Sable Island from 1995 through 2004 (Bowen et al. 2006; G. Breed and W. D. Bowen, *unpublished data*). The satellite tagging data indicated that the fraction of the Gulf of St. Lawrence and Sable Island components of the population inhabiting the ESS area varied seasonally (Table 2). Too few seals have been tagged to examine interannual patterns.

Cod abundance and biomass

As with standard fishery models, our cod population was reconstructed from catch-at-age and abundance data. Data were collected from the commercial fishery including bycatch and from four research surveys. The summer (July) survey started in 1970 and has run continuously to the present. A fall (September) survey was started in 1978 and a spring (March) survey, in 1979. Both of these surveys ended in 1984. The stratification of the spring survey was redesigned and was run from 1986 to 2002, but not in 1998. Cod length and mass were recorded for all fish, a subsample of fish were aged, and length-age keys were used to estimate mean number caught-at-age per tow. Mean numbers per tow were scaled by area swept to arrive at estimates of total abundance-at-age for the entire Eastern Scotian Shelf.

The fishery on the ESS cod stock was closed in 1993, thus the total mortality from the model is essentially natural mortality for this latter period. The model is a statistical catch-at-age model (e.g., Quinn and Deriso 1999, Savereide and Quinn 2004), structurally similar to that described in Fu et al. (2001) and is written in the same environment, AD Model Builder. However, there are a number of important differences between our model and the one presented in Fu et al. The first is how seal removals of cod are treated. In Fu et al., the removals, as had been estimated by one of two models in Mohn and Bowen (1996), are treated as data. In this study, the cod population model and the seal population model are coupled via predation, and the models are iterated until convergence to estimate seal predation mortality.

Several studies have concluded that the natural mortality of Atlantic cod has increased in recent years (Fu et al. 2001, Sinclair 2001, Fanning et al. 2003). Cod

natural mortality in Fu et al. (2001) was partitioned into immature (ages 1–4) and mature (≥ 5) categories and then modeled as a random walk. In this study, we modeled temporal increases in M with a four-parameter logistic function of time. Natural mortality was assumed to be 0.2 in 1970: the logistic slope parameter was fixed at three years, and the model estimated the inflection year and the asymptotic mortality. In addition to the data used by Fu et al., we used six more years of survey data since the closure of the fishery, providing greater insight into recent levels of natural mortality.

A total of 100 parameters were estimated by the cod population model. Cod numbers at-age in 1970 were estimated to initialize the model (12 parameters), and recruitment (age-1) from 1971 to 2003 were estimated (33 parameters). Fishing mortality was assumed to be separable and thus described by two components: selectivity (14 parameters) and annual mortality (34 parameters) (Quinn and Deriso 1999). Gear selectivity was estimated separately for the commercial fishery and the research survey over periods of gear change. The survey gear changed in the early 1980s, and the extension of jurisdiction in 1977 affected the commercial selectivity. The coefficients scaling the catch in the research survey to total population size were estimated for each period (five parameters), along with two parameters for changes in natural mortality. We present the estimates of the fit to the research survey data and the estimates of spawning stock biomass, fishing mortality rates, and natural mortality after the iterations of the seal and cod models have converged.

Seal energetics model

The daily gross energy intake (GEI; in watts) of an individual gray seal was estimated as

$$GEI_{d,a,s} = \frac{(1.7)(3.4)BM_{d,a,s}^{0.75} + TBE_{d,a,s}}{ME} \quad (6)$$

where d , a , and s index day, age (0–39 for males and females), and sex; BM is body mass (kg); ME is metabolizable energy (i.e., the proportion of the GEI available to the animal); TBE is total body energy (watts); and $3.4 \times BM_{d,a,s}^{0.75}$ is the Kleiber equation (Kleiber 1975). We multiplied the Kleiber equation by 1.7, the estimated increase in metabolism during diving, and therefore a proxy for field metabolic rate (Sparling and Fedak 2004). The Kleiber multiplier was increased to 2.5 to account for the increased metabolism of pups (Worthy 1987) and decreased to 1.07 to account for the lower energy metabolism of females during the summer (Boily and Lavigne 1995, Beck et al. 2003b). ME was assumed to be 83%, based on experimental work on seals by Ronald et al. (1984).

Lifetime changes in body mass of males and females were estimated by fitting the Gompertz growth model to data collected in the Gulf of St. Lawrence between 1988 and 1992 (Hammill, *unpublished data*; Fig. 4 in Mohn and Bowen 1996). An annual growth rate $GR_{a,s}$ was

calculated from the Gompertz curves and converted to a daily rate. These estimates were combined with estimates of seasonal changes in body mass from Beck et al. (2003a) to produce daily estimates of lifetime changes in body mass (kg):

$$BM_{d,a,s} = BM_{a,s} + g_{s,i}d + GR_{a,s}d + c \quad (7)$$

where d is the day of the year, $g_{s,i}$ is the daily rate of gain or loss in body mass over the season ($i = 1..3$ for pups and juveniles, $i = 1..4$ for adult males, and $i = 1..5$ for adult females), and c is a constant that centers the seasonal pattern on the body mass reported in Beck et al. (2003a). Modeled changes in body mass throughout the life span of males and females are shown in Fig. 2. During the first year of life, pup body mass declines from an average of 54.0 kg at weaning (Boness et al. 1995) to 37.3 kg at approximately five months of age and remains roughly constant through nine months of age (Cooper 2004). We added the daily amount of energy (watts) needed to account for seasonal changes in total body energy (TBE) to the Kleiber equation. Changes in adult TBE were modeled using estimates from Beck et al. (2003a). Seasonal changes in juvenile TBE were calculated as the energy density needed for growth (11.39 ± 0.98 kJ/d) multiplied by the daily growth rate (Bowen et al. 1999). Seals' consumption was set to 0 during times of terrestrial fasting (i.e., breeding, molt), providing more realistic estimates of seasonal food consumption by seals.

Fraction of cod in the diet

Quantitative fatty acid signature analysis (QFASA) is a method that provides estimates of diet consumed by individual seals over periods of weeks to months by estimating the proportion of prey species eaten that minimizes the statistical distance between the fatty acid composition of the predator and that of a mixture of prey (Iverson et al. 2004). Previous estimates of percentage of cod in the diet were derived from the identification of otoliths recovered from feces and stomach contents (Bowen et al. 1993, Bowen and Harrison 1994, Mohn and Bowen 1996). These estimates are known to suffer from several biases which can overestimate the fraction of the diet that consists of large, robust otoliths, such as cod (Jobling and Breiby 1986). Diet estimates from fecal samples represent mainly the last meal taken in a localized area, in our case, the immediate area surrounding Sable Island. Initial estimates were as high as 15.2% (Mohn and Bowen 1996); these were revised downward to 11.4% after the addition of subsequent data. Estimates from QFASA from 1993 to 2000 indicate that cod comprise much less of the diet of adult seals than previously thought (C. A. Beck et al., *unpublished manuscript*). Relative to adult diets, cod comprised a larger percentage of the diet of young-of-the-year gray seals. For adults, values ranged from 0% to 4.5%, while young-of-the-year values averaged 8.6% of the diet (Appendix). However, samples from young-of-the-year come only from the spring and may be biased

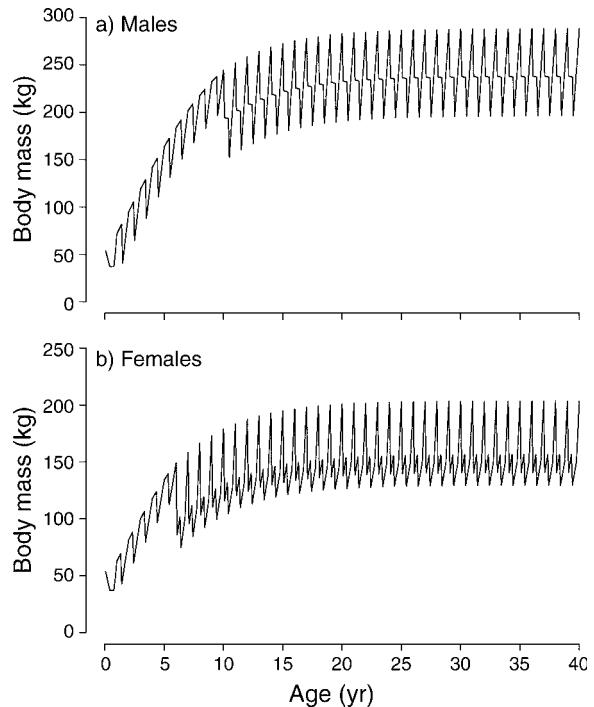


FIG. 2. Changes in gray seal body mass modeled across the lifetime of (a) males and (b) females.

upward because young seals sampled on Sable Island at this time of the year may have been foraging mainly in offshore habitats where cod is locally abundant relative to other parts of the continental shelf.

Although QFASA provides estimates of the percentage of cod in the diet, it does not provide much resolution of the size of cod consumed. Thus, we have assumed that otoliths collected from scat and stomachs represent the size distribution of cod eaten. These data indicate that smaller fish (<30 cm), rather than larger, are consumed more often by seals (Bowen et al. 1993, Bowen and Harrison 1994, 2006). We calculated the age-frequency distribution of cod consumed by seals (p_a) from otoliths collected from fecal samples from 1991 to 1997. This required that fish length be calculated from otolith length using the regression reported by Bowen and Harrison (1994), which was then assigned to an age class based on the length-at-age frequencies calculated from a sample of the entire cod population (Fig. 3). We then used the length-mass relationship to calculate the mean annual mass of a cod consumed (StomW). We assumed that the cod lengths sought by seals were constant over time, but since we know that the cod length-mass relationship changed during the study period, we calculated the mean mass of a cod consumed by seals for each year.

Consumption model

The functional response of gray seals to changes in cod density is unknown. Therefore, we analyzed our

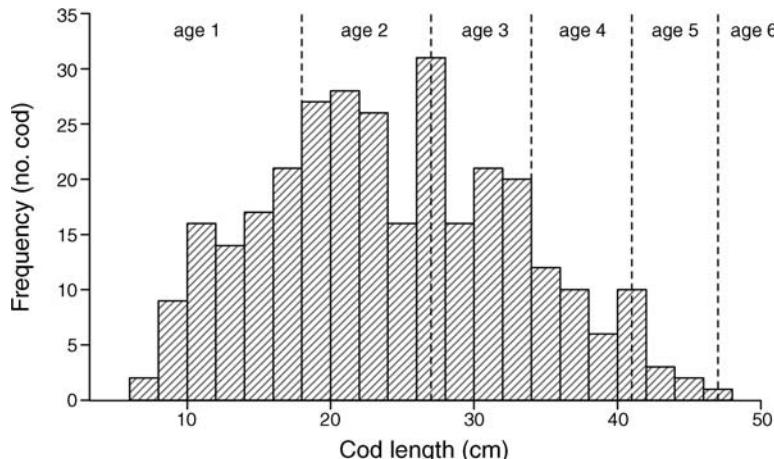


FIG. 3. The frequency of cod lengths consumed by gray seals determined from otolith length ($n = 309$). Dotted lines indicate age break points.

model under two assumptions about feeding rates. Our data on the proportion of cod in the diet, from the QFASA model, exhibited interannual variability but little evidence of an annual trend. Thus in one case, we assumed that a constant proportion of cod was eaten regardless of cod abundance (constant-ration model). Although this might be ecologically reasonable over a limited range of cod abundance, the large observed changes in cod abundance over the duration of our study make this assumption unlikely. Thus, we examined a second scenario whereby consumption rates decreased hyperbolically with cod abundance (Type 2 functional response) in view of the evidence from other predators (e.g., Assenburger et al. 2006).

The amount of biomass needed to maintain seal growth (SG) was calculated quarterly by summing the daily gross energy intake (GEI) into quarters, then dividing by the average energy (AE in kJ/g) of prey within a quarter and converting to metric tons:

$$SG_{q,a,s} = \frac{\sum_d GEI_{d,a,s}}{AE_q} (0.000001). \tag{8}$$

Recent estimates calculated from 28 prey species known to be consumed by gray seals indicate that AE varies seasonally: 5.28, 5.26, and 5.46 kJ/g for winter, summer, and fall (C. A. Beck et al., unpublished manuscript; Appendix). The total biomass (TB) of prey eaten by the seal population per quarter was calculated as

$$TB_{q,a,s} = SG_{q,1+,s}^{Sable} N_{q,1+,s} m_{q,1+,s} + SG_{q,0}^{Sable} N_{q,0} m_{q,0} + SG_{q,a,s}^{Gulf} N_{q,a,s} m_q \tag{9}$$

where N is the number of seals, and m_q is the proportion of seals remaining on the ESS during each quarter (Table 2). Since we did not have data on pup movement for the Gulf of St. Lawrence population, we assumed that pups born in the Gulf move on the ESS at the same rate as adults.

In the constant-ration model, the biomass of cod eaten (E) per quarter is a constant fraction of the total biomass consumed:

$$E_q = \sum_{a,s} TB_{q,1+,s} f_{q,1+,s} + TB_{q,0,s} f_0 \tag{10}$$

where f_{1+} is the fraction of cod in the diet of seals age-1 and older, and f_0 is the fraction of cod in the diet of young-of-the-year (mean values in Table 3). The number of cod eaten (NE) annually is then

$$NE_{t,a} = \sum_q \frac{E_q}{StomW_t} p_a \tag{11}$$

where StomW is the mean mass of cod consumed from 1970 to 2003, and p_a is the proportion of cod consumed at-age. From the otolith data for the period 1991–1997, we calculated $p_a = (0.341, 0.344, 0.217, 0.076, 0.018, 0.003)$ (Fig. 3).

We formulated the functional-response model by calculating an interaction coefficient (q_a) between the number of seals and the number of cod across age classes. Since there was no evidence of an annual trend in the proportion of cod in the diet for years with QFASA diet information (1993–2000), we calculated our interaction coefficient at the start of the QFASA data series. First we calculated the number of cod consumed at-age in 1993 as

$$nc_a = \frac{\bar{E}}{StomW} p_a \tag{12}$$

where \bar{E} is the mean biomass of cod eaten from the constant-ration model for 1993. The interaction between cod and seals was then calculated as follows:

$$q_a = \frac{nc_a}{C_a \bar{N}} \tag{13}$$

where C_a is the mean number of cod-at-age, and \bar{N} is the mean number of seals on the ESS in 1993. It is often

TABLE 3. Age- and sex-specific abundance, daily energy intake, daily food intake, and annual food intake of gray seals on the ESS in 2003.

Age (years)	No. seals in 2003		Daily energy per individual (W)		Daily food per individual (kg)		Annual population consumption (metric tons)	
	Male	Female	Male	Female	Male	Female	Male	Female
0	17 399	17 399	208	206	3.18	3.15	20 199	19 999
1	10 111	10 499	168	152	2.73	2.46	10 062	9 442
2	7 827	8 125	206	182	3.34	2.97	9 553	8 794
3	6 136	6 368	240	210	3.91	3.42	8 761	7 943
4	4 871	5 054	272	235	4.42	3.82	7 865	7 047
5	3 913	4 059	300	257	4.88	4.18	6 967	6 185
6	3 177	3 294	324	250	5.28	4.04	6 119	4 856
7	2 603	3 139	346	260	5.63	4.21	5 345	4 818
8	2 151	2 955	364	269	5.93	4.34	4 652	4 687
9	1 789	2 747	380	276	6.19	4.46	4 040	4 471
10	1 496	2 518	389	282	6.31	4.55	3 445	4 186
15	1 106	1 373	419	298	6.80	4.82	2 747	2 415
20	593	645	430	304	6.98	4.91	1 512	1 155
25	283	296	434	305	7.04	4.94	726	533
30	133	138	435	306	7.06	4.95	344	249
35	65	67	436	306	7.07	4.95	168	121
39	37	38	436	306	7.07	4.95	96	69
Total	75 377	83 376	391†	284†	6.34†	4.59†	121 600‡	112 655‡

† Average over all ages.

‡ Mean field approximations were used to calculate annual population consumption. The estimates of total consumption in Table 4 are more accurate.

observed that predator consumption rates increase with prey density up to a maximum level. We parameterized a hyperbolic functional response by assuming that the proportion of cod calculated from scat from 1991–1997 represented the maximum proportion of cod in a seal’s

diet. This assumption seems reasonable because gray seal scats represent short-term diet from foraging trips close to Sable Island, which is an area where cod are commonly found (Fanning et al. 2003). We calculated the asymptotic attack rate ($q_{a,max}$) by setting $f_{1+} = 0.22$ and recalculating q as

$$q_{a,max} = \frac{nc_a}{N}. \tag{14}$$

We assumed that each q_a derived from QFASA provides an accurate estimate of attack rates at low cod abundance. If we then assume a hyperbolic functional response, the number of cod eaten is given by

$$NE_{t,a} = \frac{q_a C_{t,a}}{1 + \frac{q_a C_{t,a}}{q_{a,max}}} \left(N_t \frac{\text{Stom}W_t}{\overline{\text{Stom}W}} \right) \tag{15}$$

where $\overline{\text{Stom}W}$ is the mean mass of cod consumed over 1971–2003. Fig. 4 shows the functional response of seals to age-1 and age-2 cod.

Estimating parameter uncertainty

The model incorporates parameter uncertainty in two ways. The means and variances of several parameters in the seal population dynamics model were estimated directly from the pup count data (Table 1), by minimizing an objective function that is the negative-log likelihood for observed vs. predicted pup numbers. However, the majority of parameters were taken from other studies (Appendix). For these parameters, a probability density function was calculated and converted into a negative-log likelihood. These likelihoods were added to the objective function and acted as penalty functions (Breen et al. 2003). In both cases,

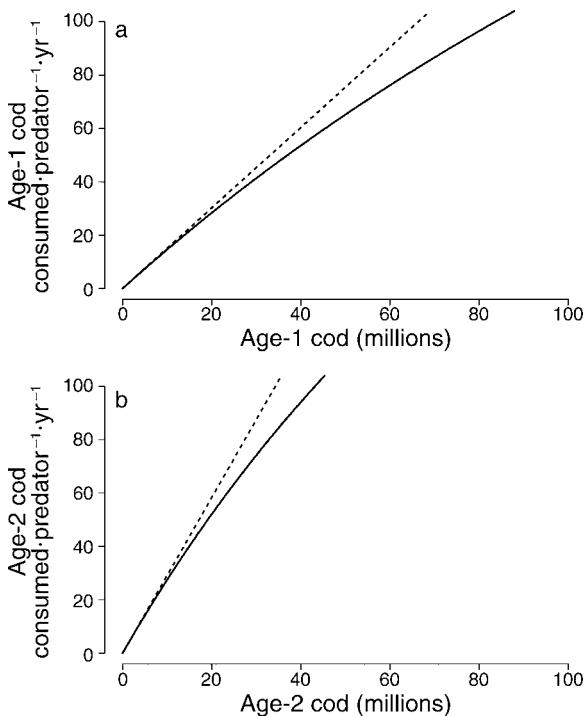


FIG. 4. The functional response (solid line) of gray seals to (a) age-1 and (b) age-2 cod. The linear functional response (dotted line) was not used but was added for comparison.

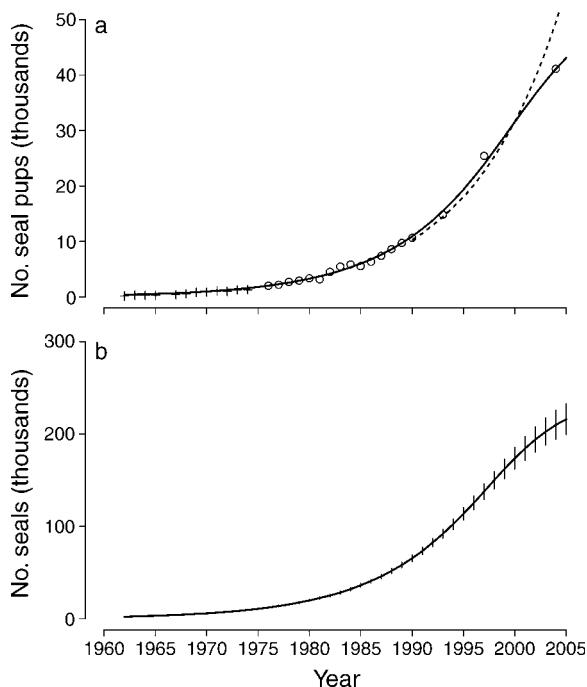


FIG. 5. (a) Census counts (circles) and model fit (solid line) to the pup production of the Sable Island gray seal population. In early years, only partial censuses (plus symbols) were completed. These data were added to the plot for reference but were not fit to by the model. The model of exponential increases (dotted line) was not used but was added for comparison. (b) Model estimates of total population size. Vertical lines indicate the 95% CI.

variances from the Hessian matrix are carried through the model and are reflected as uncertainty in the final estimates of consumption. Consequently, a large amount of variability has been incorporated into the model from a wide variety of sources. This variability can be broadly categorized into uncertainty in gray seal (1) population dynamics, (2) energetics, and (3) cod consumption. Several sources of error were not included, as each model component contains a few fixed values (Table 1, Appendix). Variability in the cod model was incorporated by running the seal model at ± 1 SE of cod numbers at-age. We present the range in mortality estimates due to seal predation and other sources.

RESULTS

Gray seal (*Halichoerus grypus*) populations have continued to increase on Sable Island, but the 2004 estimate suggests that the rate of increase in pup production has slowed (Fig. 5). In the Gulf of St. Lawrence, pup production also increased over time, with the 2004 estimate the highest in the series (Hammill and Gosselin 2005; Fig. 6). The carrying capacity of the Sable Island population was estimated at 430 000 gray seals, with the density-dependent parameter, θ , held constant at 2.4 (Trzcinski et al. 2005). Combining estimates of total population size with estimates of

seasonal movement patterns, the model predicted a steady rise in the number of gray seals using the study area from fewer than 8494 seals (± 691 SE) in 1970 to 158 750 seals (± 7186 SE) in 2003 (Fig. 7). However, there was also a strong seasonal signal, such that numbers in 2003 varied from about 128 000 in summer to 182 000 in winter (Fig. 7).

Fig. 8a shows the fit to the cod abundance estimates from four-survey series. The Atlantic cod (*Gadus morhua*) numbers show continued decline since the early 1980s. Spawning stock biomass is shown in Fig. 8b. Current estimates for either number or biomass are the lowest in the entire 34-year time series, despite the closure of the fishery in 1993 and low fishing mortality rates thereafter (Fig. 8c). We estimated a spawning biomass of 6524 t (1 SE: 2180–20 547 t) in 2003, and our overall trends are in broad agreement with those reported in previous assessments (Fu et al. 2001, Fanning et al. 2003). Since 1984, the spawning biomass has fallen more rapidly than the number of cod, indicating a change in the age and size structure of the cod population, and resulting in a larger proportion of the dwindling stock becoming available to seal predation (Fig. 8b).

The energetics model estimated that, on average, males consumed 1.61 tons and females 1.35 tons of food per year (Table 3). Young-of-the-year comprised $\sim 22\%$ of the gray seal population. Yet, despite their smaller size, they consumed $\sim 17.7\%$ of the total prey biomass. Total consumption varied seasonally, but the three age-sex classes showed contrasting patterns (Table 4). Consumption by young-of-the-year, as a proportion of the total, was highest in the first quarter and lowest in the third and fourth quarters. Consumption by adult males was fairly consistent across the first three quarters, then increased in the last quarter, whereas consumption by adult females was high in the first quarter (i.e., post-reproduction), low in second and third quarters, and highest in the fourth quarter. The increase in consumption by adult males and females in the fourth quarter was caused by the rapid increase in body energy storage leading up to the breeding season (Beck et al. 2003a).

Under the assumption of a constant ration of cod, the model estimated that 29.3 (± 9.0 SE) million cod were consumed by seals in 2003 (Fig. 9b), corresponding to a mass of 5369 (± 9519 SE) metric tons. By comparison, the functional-response model estimated that 16.7 (± 27.7 SE) million cod were consumed in 2003 (Fig. 9), corresponding to 2899 (4888 SE) tons. In 2003, the functional-response model estimated that each seal consumed 97 cod (i.e., 50.4, 36.5, 5.3, 4.4, and 0.7 cod at ages 1–5, respectively).

Prior to 1995, the instantaneous mortality rate of cod (ages 1–5) due to seal predation was low, averaging less than 0.01. Seal predation mortality rates increased as the seal population grew and the cod population further declined. The functional-response model estimated seal predation mortality to average 0.21 since the closure of

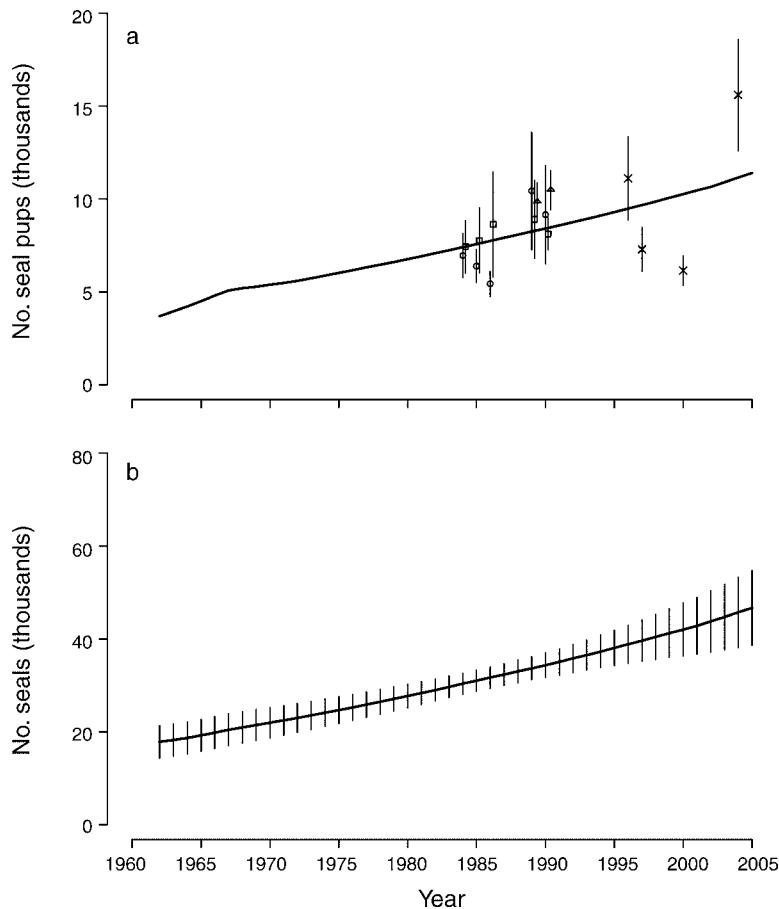


FIG. 6. (a) Census counts and model fit (solid line) to the pup production of the Gulf of St. Lawrence gray seal population. Symbols represent four data sets collected using different methods; estimates were calculated from pups recaptured at Anticosti Island (circles), Sable Island (from Hammill et al. 1998; squares), from Myers et al. (1997a; triangles), and aerial survey methods (Hammill and Gosselin 2005; × symbols). Vertical lines indicate ±SE. (b) Model estimates of total population size. Vertical lines indicate the 95% CI.

the fishery (across ages 1–5) and 0.31 in 2003 (Fig. 10). Although fecal data indicated that gray seals consume cod ages one to eight, the highest mortality rates occurred on cod aged two, three, and four (i.e., 0.35, 0.28, and 0.19 since 1993). We estimated that instantaneous natural mortality due to factors other than gray

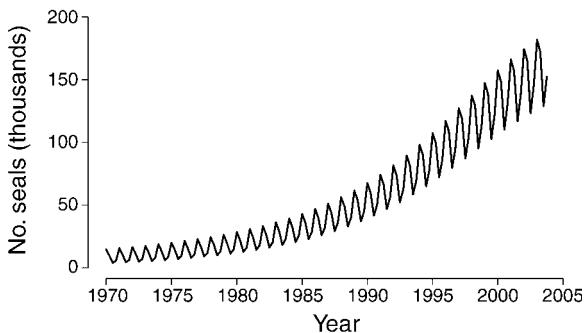


FIG. 7. Estimated total number of gray seals on the ESS (Eastern Scotian Shelf) accounting for population trends and immigration and emigration.

seal predation was 0.78 in 2003 and has averaged 0.62 since 1993. Therefore, the functional-response model estimates mortality due to gray seals on two, three, and four year old cod was 57%, 46%, and 30% of the natural mortality attributed to other causes (or 36%, 31%, and 23% of all mortality including bycatch mortality).

Seasonal consumption of cod by seals varied with seal age and sex. Current data indicate that adult males did not consume measurable amounts of cod in the second quarter and consumed the most cod in the fourth quarter. In contrast, females consumed the greatest proportion of cod in the second and third quarters leading up to the breeding season (Table 5). Overall, young-of-the-year consumed the most cod, adult males the least, and adult females consumed approximately three times more than males (Table 5).

The Gulf of St. Lawrence population had a relatively minor predation impact on the ESS, consuming only 8.8% of the total biomass and 7.5% of the cod. Although comparatively low, their impact peaked in the fourth

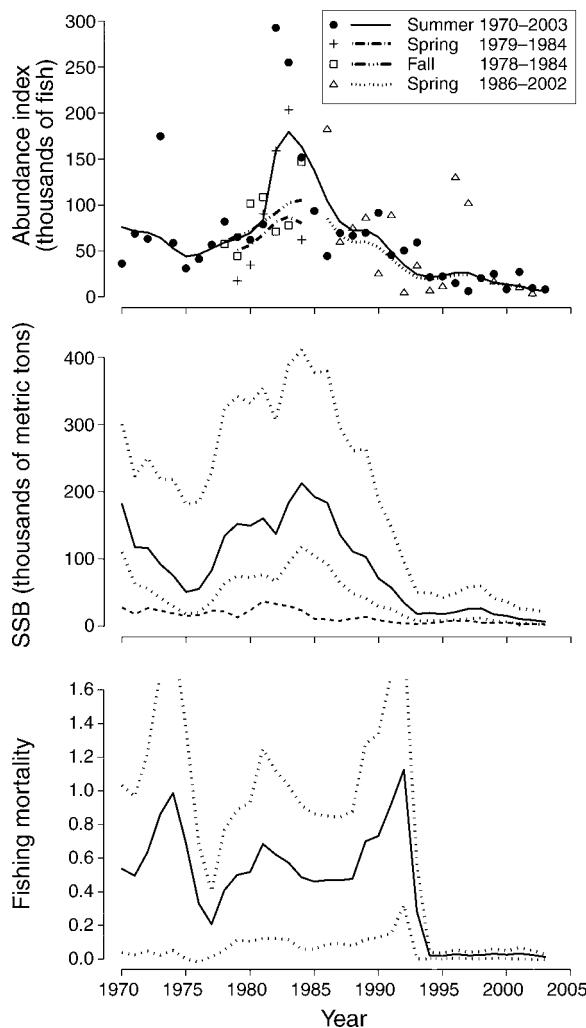


FIG. 8. (a) Abundance index in four research surveys (points) and predicted by a statistical catch-at-age model (lines). (b) The estimated trends in cod spawning stock biomass (SSB; solid line) and the biomass of cod selected by seals (dashed line) (1 metric ton = 1 Mg). (c) The instantaneous fishing mortality for fully selected ages. Dotted lines in (b) and (c) are \pm SE.

quarter with the migration onto the ESS, presumably in response to the formation of ice in the Gulf of St. Lawrence (Table 2; G. Breed and W. D. Bowen, unpublished data).

Our uncertainty in the amount of cod consumed by gray seals is large. For example, the functional-response model estimated that 16.7 million cod were consumed by seals in 2003 (Fig. 9b), but 1 SE is ± 27.7 , making the 95% confidence limits on that estimate approximately ± 55.4 million cod. Despite our uncertainty about seal predation mortality (i.e., our estimate includes 0 because of the high uncertainty in the consumption term [neither cod nor seals include 0]), the model indicates that gray seals accounted for a small but perhaps significant fraction of the natural mortality from other sources

(Fig. 10). The contribution of the uncertainty in gray seal population dynamics and the number of seals foraging on the ESS to our uncertainty in cod consumption was small (Fig. 11a) compared with our uncertainty in gray seal energetics (Fig. 11b) and diet (Fig. 11c). By far the greatest uncertainty in our estimate of cod consumption is due to our uncertainty in cod population dynamics (Figs. 8 and 12). Variation in cod numbers at-age affects both the strength of the interaction coefficient calculated in 1993 and our estimate of the impact of gray seal predation on cod population recovery.

DISCUSSION

Predators in both terrestrial and marine systems have been blamed for the declines of many species of commercial or recreational value (Punt and Butterworth 1995, Yodzis 1998, Treves and Karanth 2003, Woodroffe et al. 2005). Proposals to reduce predator populations come from the notion that they are the principal source of natural mortality. While this may be true in some cases (Sinclair et al. 1998, Courchamp et al. 2003, Wittmer et al. 2005), in others it is not (Punt and Butterworth 1995, Valkama 2005). Our model indicates that during the 11-yr period of the fishing moratorium (i.e., through 2003) there is little evidence that gray seals (*Halichoerus grypus*) were the principal source of natural mortality on the ESS Atlantic cod (*Gadus morhua*) stock. Although any mortality on a depleted population undergoing further decline is detrimental to population recovery, even the complete removal of gray seal predation would not assure the recovery of the cod population, given the high levels of other sources of natural mortality. We estimate that current instantaneous natural mortality rates of young fish (ages 1–5), after accounting for seal predation, is 0.78, which is similar to our estimates of fishing mortality on older fish (>5) during the heyday of the fishery.

Although we are still uncertain about both elements of model structure and some parameters of the model, several improvements have been made to the predation model of Mohn and Bowen (1996). In the earlier model, the seasonal fraction of the Sable Island and Gulf of St. Lawrence components of the population that foraged on the ESS was largely unknown. Satellite telemetry studies

TABLE 4. Estimated annual consumption of biomass by the gray seal population on the ESS for 2003.

Category	Total biomass (metric tons)	Proportion of biomass consumed, by quarter			
		First	Second	Third	Fourth
YOY	40 850	0.37	0.29	0.17	0.17
Male	98 729	0.24	0.21	0.24	0.31
Female	91 334	0.29	0.17	0.17	0.37
Total	230 912	0.28	0.21	0.20	0.31

Notes: Annual consumption was partitioned into three population categories and the proportion consumed by quarter.

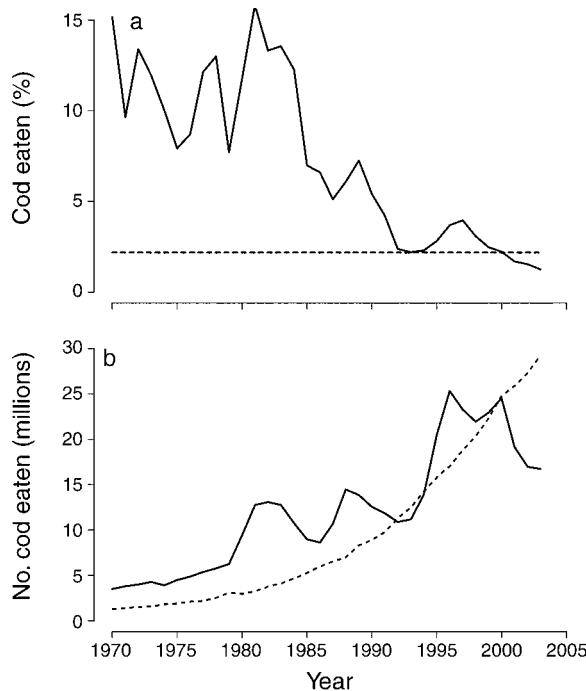


FIG. 9. Results of the constant-ratio (dashed line) and the functional-response (solid line) models for (a) the percentage of cod in a gray seal's diet and (b) the number of cod eaten by the ESS gray seal population.

have provided empirical estimates of the seasonal distribution, and it is now evident that many gray seals make long foraging trips far beyond the ESS (Austin et al. 2004; Table 2) and that the seasonal use of the ESS varies by sex and age group. The bioenergetic model now includes good estimates of the metabolic cost of diving (Sparling and Fedak 2004), a growth premium calculated from the Gompertz curve, and seasonal variation in body mass and total body energy (Beck et al. 2003a), all of which result in better estimates of the seasonal energy requirements of the population.

Another important improvement in our model is the new estimates of proportion of cod in the diet of gray seals derived from QFASA (Iverson et al. 2004; C. A. Beck et al., *unpublished manuscript*; Appendix). QFASA presumably provides a more accurate population level estimate of proportion of cod in the diet because it integrates consumption over a broader spatial domain and a time frame from weeks to months (Iverson et al. 2004). By contrast, scat and stomach contents estimates, used in the earlier model (i.e., Mohn and Bowen 1996), provide information mainly on the last meal eaten within 100 km of the collection site (Bowen and Harrison 1994). This means that gray seal diet in a large fraction of the ESS cannot be investigated using scats or stomach contents. Nevertheless, otoliths collected from scats and stomach contents provided critical information on the length of prey eaten (Bowen and Harrison 1994, 2006; Fig. 3). Thus, given the difficulty in

estimating the diet of pinnipeds, the use of multiple methods is valuable.

QFASA is a new method for estimating the diet of predators. As with any method, it has strengths and weaknesses. As noted above, one of the strengths of the method is that it provides information on the diet of individuals over ecologically relevant spatial and temporal scales. However, the method relies on having good estimates of the fatty acid composition of potential prey and the fact that prey species eaten have distinct fatty acid signatures. If prey eaten by the predator is not included in the QFASA model, it will not be identified. Evidence to date indicates that potential gray seal prey can be reliably distinguished (Budge et al. 2002). Furthermore, gray seal diets were estimated using a prey library of 28 species of fish and invertebrates from the study area that were either known (from scats or stomachs) or suspected (because of abundance and depth availability) to be eaten by this species (C. A. Beck et al., *unpublished manuscript*).

Lastly, we have added a hyperbolic functional response to the predation model. Although the parameters of the response are guided by data, they are clearly provisional. The hyperbolic functional response is commonly observed in predators (Murdoch and Bence 1987, Turchin 2003), including pinnipeds (Mori and

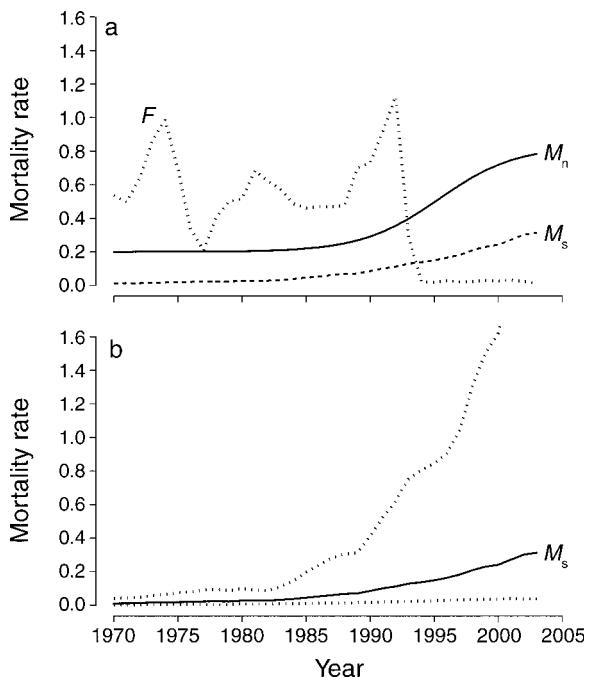


FIG. 10. (a) The instantaneous fishing mortality rate for fully selected fish (F , dotted line), estimated increase in natural mortality (M_n) for ages 1–5, and estimated trend in seal predation mortality (M_s) of cod ages 1–5 from the functional-response model. (b) The estimated instantaneous mortality rate caused by gray seal predation. The dotted lines in (b) are $\pm SE$, estimated from the Hessian approximation of the variance-covariance matrix.

TABLE 5. Estimated annual consumption of cod biomass by the gray seal population on the ESS for 2003. Annual consumption was partitioned into three population categories and the proportion consumed by quarter.

Category	Constant-ration biomass (metric tons)	Functional-response biomass (metric tons)	Proportion of biomass consumed, by quarter			
			First	Second	Third	Fourth
YOY	3507	1897	0.34	0.29	0.18	0.19
Male	484	262	0.20	0.17	0.00	0.63
Female	1370	741	0.08	0.05	0.51	0.37
Total	5361	2899	0.26	0.22	0.25	0.27

Boyd 2004, Assenburog et al. 2006). The largest effect of including a hyperbolic function response was to constrain consumption rates when cod were abundant in the 1980s. However, even in recent years the functional-response model predicted only 54% of the cod consumption estimated by the constant-ration model (Fig. 9, Table 5). This underscores the importance

of further research on the functional responses of gray seals.

We have included a measure of variability in most of the parameters in the model (Table 1, Appendix). This variability is clearly reflected in the width of the confidence limits on our estimates of gray seal predation mortality. Nevertheless, we have certainly not included all sources of variability in model parameters. We also examined model structure in relation to the form of the functional response. However, we have assumed that density dependence takes the form of reduced pup and juvenile survival. Although this is a reasonable assumption based on analogy to other mammals, we have no evidence to support this assumption in the case of our population. Other forms of density dependence, say reductions in fecundity, could have large effects on our estimate of gray seal population size and, in turn, on estimates of predation mortality. However, we have no data on changes in fecundity.

We did not reexamine the sensitivity of our model to input parameters, but we expect the relative importance of parameters would be similar to the earlier model by Mohn and Bowen (1996: Table 10) because of the structural similarity of the two models. Based on the earlier model, estimates of cod consumption, and thus predation mortality, are expected to be most sensitive to changes in the size of the seal population, the composition of seal diet, and seal metabolic rates.

It is becoming widely recognized by ecologists that heterogeneity in predation pressure in both time and space can have impacts on prey populations that are not evident in simpler models (Hassell 2000, Alonzo et al. 2003, Jackson et al. 2004). Thus, an important result of our model is the strong seasonal pattern of predation on cod. The impact of gray seal predation on the ESS cod population appears to be greatest just prior to and following the breeding season (fourth and first quarters), which corresponds to the aggregation of the population near the breeding colony on Sable Island and the initial foraging trips of weaned pups. Consequently, the impact of gray seals on cod is spatially diffuse over much of the year, but during the breeding season the impact increases in intensity in the vicinity of Sable Island. This temporal and spatial variation in gray seal predation could have important effects on the recovery of the cod population, if the region surrounding Sable

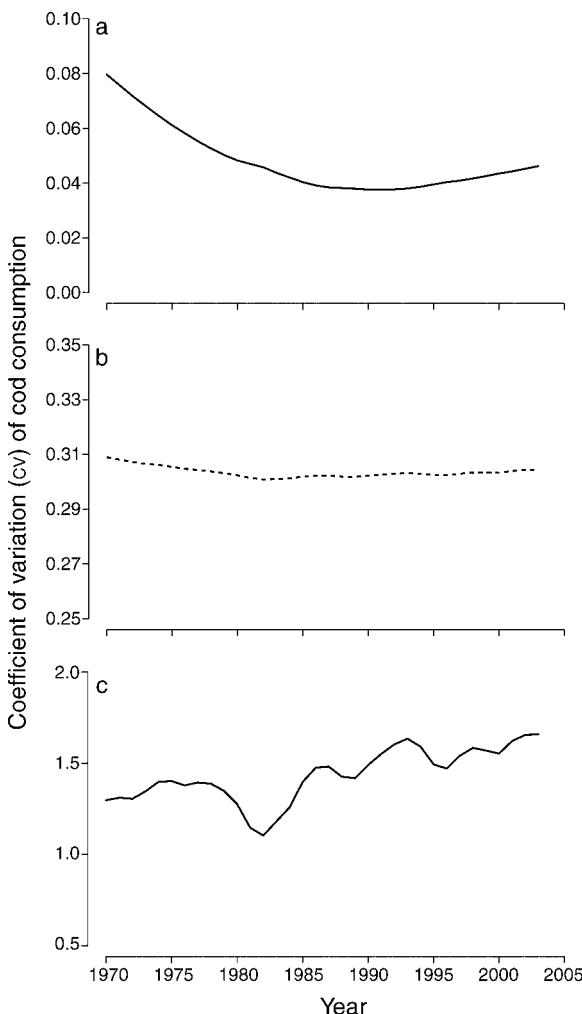


FIG. 11. The contribution of the uncertainty in (a) gray seal population dynamics; (b) population dynamics and energetics; and (c) population dynamics, energetics, and diet on the coefficient of variation (cv) of cod consumption.

Island is a cod spawning or nursery area. At times, high densities of eggs and larvae have been found near Sable Island in ichthyoplankton surveys, but the data are too sparse to determine the importance of this area to cod reproduction (Department of Fisheries and Oceans, Canada; Stewart et al. 2003).

Generalist predators can drive alternative prey to extinction (Murdoch and Bence 1987, Holt and Lawton 1994, Wittmer et al. 2005; but see further discussion later in this paper). To the extent that gray seals consume cod, they are having a negative impact on the recovery of the declining ESS cod stock. Of course, any removal of individuals from a population which has exponentially declined at a rate of 17% per year for 10 years would be detrimental to population recovery, whether by concurrent fisheries, by seals, or other sources of natural mortality. However, QFASA estimates of diet indicate that gray seals consume relatively little cod, and that sand lance (*Ammodytes dubius*) and redfish (*Sebastes* spp.) account for most of their diet (Bowen et al. 2006). There is also some evidence that gray seals do not positively select for cod relative to their abundance (Bowen and Harrison 2006), which has also been observed in harp seals (Lawson et al. 1998).

Why cod stocks, including the ESS stock, showed rapid recovery after fishing pressure was reduced in 1977 with the introduction of the 200-mile limit and not after the closure of the fishery in 1993 remains poorly understood. Many things have changed in the ESS ecosystem over the study period (1970–2003), including fishing practices, the age structure of cod, the abundance of predators, and sea temperature (Zwanenburg et al. 2002, Choi et al. 2004, Frank et al. 2005). The current state, where pelagic fish and seals are abundant, presumably makes it more difficult for cod to survive early life stages (Swain and Sinclair 2000, Walters and Kitchell 2001). However, cod feed on many members of the community (Link and Garrison 2002), making it difficult to predict their response to changes in the seal population or fishing pressure (Yodzis 1998, 2000). Generalist predators, such as gray seals, can actually have a positive impact on less preferred prey through indirect interactions (Punt and Butterworth 1995, Yodzis 1998). Much focus has been placed on recruitment variability and the high mortality of young cod, but few have explained the increased mortality in older (5+) cod observed by Fanning et al. (2003). Large cod and seals have considerable dietary overlap (Link and Garrison 2002; C. A. Beck et al., *unpublished manuscript*) and could be competing for common resources.

The abundance of Atlantic cod on the ESS has decreased exponentially at a rate averaging 17% per year over the past several decades. In addition to this recent decline, there is strong evidence, based on historical catch data, that this stock has decreased substantially over several centuries (Myers et al. 2001, Rosenberg et al. 2003). In the several decades prior to the 1980s, seal predation must have had little impact on the abundance

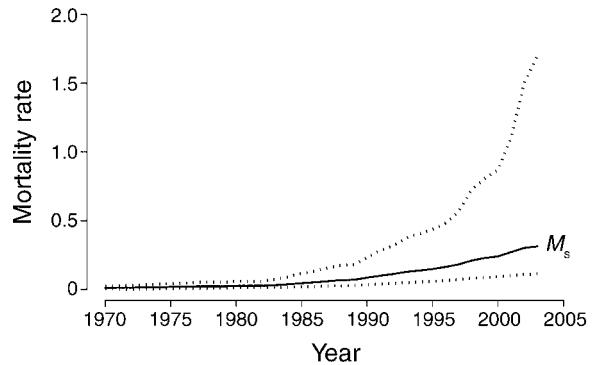


FIG. 12. The contribution of the uncertainty in cod population dynamics on the estimated trend in seal predation mortality (M_s) on cod ages 1–5 from the functional-response model. The solid line is the mortality estimated at the best estimate of cod numbers at-age (matrix of estimated cod abundances for ages 1–12 over the study period). Variability, shown as dotted lines, was calculated by running the seal model at ± 1 SE of cod numbers at-age.

and dynamics of this cod stock, given that there were so few seals. Presumably, the current state of this cod stock is largely the result of the long-term effects of overfishing (Hutchings and Myers 1994, Hutchings 2005), rather than the relatively recent increase in gray seals.

The closure of the cod fishery and the continuation of trawl surveys allowed us to better estimate the natural mortality of cod (Trzcinski et al., *unpublished manuscript*). However, it is still very difficult to estimate natural mortality, particularly on young fish and while the cod population is rare. Our estimate of impact, the ratio of mortality due to seal predation to natural mortality, is sensitive to our assumptions about natural mortality. While it is clear that natural mortality has increased, it is difficult to say by how much. This information is important in understanding the current state of the cod population, and its potential for recovery, while allowing us to place the mortality caused by gray seals in perspective.

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APPENDIX

Values used in simulation model (*Ecological Archives* A016-073-A1).