



Seal–cod interactions on the Eastern Scotian Shelf: Reconsideration of modelling assumptions

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ABSTRACT

The cod stock on the Eastern Scotian Shelf (the 4VsW management area) collapsed in the early 1990s, and has experienced high natural mortality since then, while the abundance of grey seals foraging in the area has doubled about every seven years since the 1960s. The causes of the high cod natural mortality are not well understood, but seals are not considered to have played a significant role. This study takes a fresh look at the impact of seals on 4VsW cod abundance. Abundance trends of the Sable, Eastern Shore and Gulf seal herds which forage on the Scotian Shelf are estimated to 2020. The Sable herd is projected to stabilize at about 350,000 individuals. If their exponential growth continues, the Eastern Shore and Gulf herds could in aggregate reach about 200,000 individuals. However, density dependent processes are likely to slow population growth of these two herds sometime in the coming decade. Total annual food consumption of the three herds is estimated. In 2010, in excess of 550,000 t of fish are consumed annually by the Sable and Eastern herd, with the Gulf herd consuming about 138,000 t. The literature on seal diets is summarized and three scenarios of type II predator–prey functional response are defined. In an ADAPT analysis of the 4VsW cod stock, seals are treated as an additional fishing gear sector under two scenarios: respectively a “flat-top” and “domed” partial recruitment vectors. Model results infer that seals have contributed to increases in natural mortality since the late 1980s, and have contributed to the lack of recovery of the stock since 1993. However, predictions by the functional models are not consistent with estimate of recent increases in abundance of cod in trawl surveys. Present levels of grey seal abundance have not occurred on the Scotian Shelf since at least the 1800s.

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1. Introduction

Interpretation of the collapse of the cod stocks off Atlantic Canada, as well as their lack of recovery in spite of fishery closures and severe fisheries restrictions, continues to be controversial. The geographic and temporal patterns are complex, with the degree of the declines and their timing varying considerably amongst the cod management areas in the northwest Atlantic. This paper focuses on the impact of grey seals (*Halichoerus grypus*) on Atlantic cod (*Gadus morhua*) on the Eastern Scotian Shelf (4VsW management area) off Nova Scotia, Canada (Fig. 1).

Natural mortality of cod, and of several other fish species, in this geographic area has been exceptionally high in recent decades. As it is difficult to separate natural mortality from fishing mortality (particularly when there are directed fishing activities underway), the estimates of temporal and spatial patterns of cod natural mortality are approximate in nature. Halliday and Pinhorn (2009) provide a

review of changes in natural mortality for a number of fish species in the northwest Atlantic. They conclude that the increases preceded the fishery closures in 1992/1993. The 4VsW cod stock has continued to decline in spite of the closure of a directed fishery since 1993. Research surveys indicate that high levels of total mortality have continued, even after closure of the 4VsW cod fishery in 1993, implying that natural mortality has been exceptionally high during the past two decades. However, since 2006, there has been an increase in the survey trawl estimates of cod biomass and an associated decrease in the estimates of natural mortality (Fig. 2).

Coincident with the increase in natural mortality of cod (and other fish species), there has been an additional relatively unique marine ecological phenomenon. Grey seal pup production on Sable Island has been increasing by about 13% annually since the early 1960s (Bowen et al., 2003), while the Gulf of St. Lawrence component of the population complex has been increasing at 7.4% annually (Hammill et al., 1998). Grey seal abundance on Sable Island has been growing exponentially for four decades, doubling about every seven years, as has their annual food consumption. Exponential growth over several decades is rarely observed in the nature. The coincidence of these two observations – the dramatic changes

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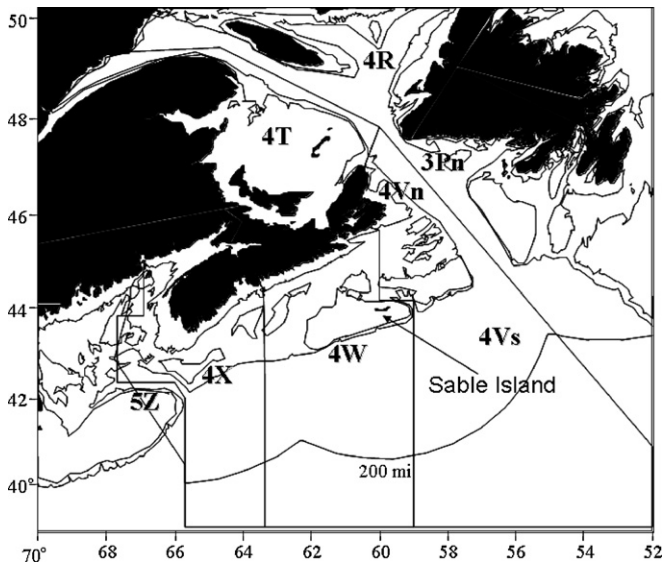


Fig. 1. Gulf of St. Lawrence (4T and 4Vn), Eastern Scotian Shelf (4Vs and 4W), Western Scotian Shelf (4X) and Georges Bank (5Z); Sable Island is indicated in 4W.

in natural mortality of cod and the exponential growth of a top predator (from about 3000 seals on Sable Island in 1960 to over 300,000 in recent years) – has generated speculation by the general public and fishing industry that the two phenomena may be connected. In particular, the fishing industry feels strongly that grey seals are responsible for the increases in natural mortality of cod (and other fish species of commercial importance). That said, they accept that overfishing had also occurred prior to the 1993 closure.

There have been several evaluations of the impact of grey seals on the cod stocks off Atlantic Canada. Mohn and Bowen (1996), based on a “minimum realistic” predator/prey model for the Eastern Scotian Shelf area (4VsW) for the 1970–1994 period, concluded that grey seals were not a major factor in the collapse of the stock. Sinclair et al. (1997), based on a comparative analysis of fisheries management practices on the Eastern (4VsW) and Western (4X) Scotian Shelf, concluded that a combination of poor environmental conditions and increases in natural mortality (in part due to seal predation) had contributed to the decline in stock production and recruitment. Fu et al. (2001) evaluated the causes of the lack of

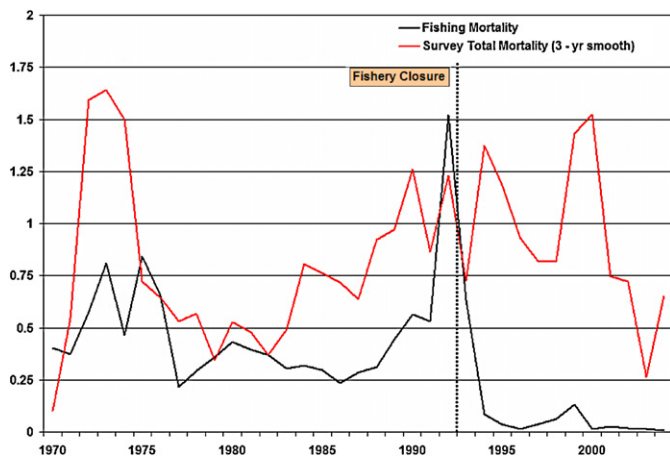


Fig. 2. Trends in adult fishing and total mortality of 4VsW cod during 1970–2005; the total mortality estimates (3-year smooth of age 5–7) are derived from the research vessel trawl survey catches; the closure of fishery in 1993 is indicated; after 1992, total mortality is an estimate of natural mortality.

recovery of cod on the Eastern Scotian Shelf following the 1993 fishery closure. They concluded that seal predation was not a significant factor. Trzcinski et al. (2006) also focused on the lack of recovery of cod since 1993. They concluded that grey seals had made some contribution to increases in cod rates of natural mortality (0.21 yr^{-1}) in the post fishery closure period, but that “unknown sources of mortality (0.62 yr^{-1}) are contributing to the failure of cod to recover”. Trzcinski et al. (2009) updated their model, and included an analysis of the Western Scotian Shelf (4X) management area. For both management areas, they conclude that seal predation on cod is a minor contribution to natural mortality. Again, other unknown sources are concluded as having caused the stocks to decline (in 4X where there is an ongoing fishery) and to not recover (in 4VsW which has been closed to cod fishing since 1993).

Bundy (2004), and Bundy and Fanning (2005), developed an Ecopath mass-balance model of the Eastern Scotian Shelf to compare the pre-collapse (1980–1985) and post-collapse (1995–2000) periods. The results indicated high predation mortality on both small (<40 cm) and large (>40 cm) cod (i.e. the Ecopath model confirmed the increases in natural mortality that had been estimated from the research vessel surveys and in other models). The sources of the high natural mortality for the large cod were unaccounted for, and Bundy (2004) concluded that their Ecopath model had not helped to explain this phenomenon. Furthermore, Bundy and Fanning (2005) concluded that grey seals cannot account for the high levels of “unaccounted for” natural mortality of cod estimated from the model. Bundy et al. (2010) expanded the Ecopath modelling through a comparative analysis of four geographic areas off Atlantic Canada (Newfoundland and Labrador Shelf, Northern Gulf of St. Lawrence, Southern Gulf of St. Lawrence, and the Eastern Scotian Shelf). Although they conclude that seal predation is a significant cause of the elevated natural mortality of cod for three of the areas, this was not considered to be the case for the Eastern Scotian Shelf management area. This is a paradoxical conclusion given that the rate of increase of grey seal abundance during the time period of the analysis is higher in the 4VsW management area than in 4TVn. Also, the other seal species of importance as predators in the northern Gulf and the Newfoundland and Labrador shelves (harp and hooded seals) have not been increasing at as high a rate as that for grey seals.

For the Southern Gulf of St. Lawrence, Chouinard et al. (2005) and Swain and Chouinard (2008), on the basis of correlations of trends in natural mortality of cod and abundance of grey seals, conclude that there is a tight correspondence. They note, however, the anomaly that high natural mortality is estimated for cod greater than age 3, whereas the diet of grey seals is estimated to comprise mostly juvenile cod (ages 1–3).

In summary, the scientific literature on the impacts of grey seals on the temporal trends in natural mortality and abundance of cod does not support the interpretations of the fishing industry on the observed dramatic ecosystem changes on the Scotian Shelf during the past three decades. To the degree that there is a scientific consensus, grey seals are not considered to have been a significant predator of cod on the Scotian Shelf. Grey seals are, however, considered to be a major contributor to the increase in natural mortality in the southern Gulf of St. Lawrence (Bundy et al., 2010; Chouinard et al., 2005; Swain and Chouinard, 2008). With the exception of Sinclair et al. (1997), no studies conclude that grey seals have contributed to the collapse of the cod stocks in this area during the late 1980s and early 1990s.

Given the contradictions amongst geographic areas in the interpretations of the role of grey seals on cod population trends, and the unexplained increase in natural mortality of cod on the Eastern Scotian Shelf since the late 1980s, this paper re-evaluates the impacts of grey seals on cod on the Eastern Scotian Shelf. The following aspects are addressed:

- Grey seal abundance trends for the Sable Island, coastal Eastern Nova Scotia, and Gulf of St. Lawrence herds.
- Total annual food consumption by each herd, by season and geographic area.
- Density dependent functional response of seal predation on cod.
- Size and age selectivity of cod consumed by grey seals.
- Population trends of cod on the Eastern Scotian Shelf from 1970 to 2009, including estimates of the contribution of grey seal predation to cod natural mortality.

2. Grey seal abundance trends

As seals from the three herds (Sable Island, Eastern Nova Scotia, and the Gulf of St. Lawrence) forage on the Eastern Scotian Shelf for parts of the year, it is necessary to estimate abundance trends for all the herds and then estimate the fractions that feed on the Eastern Scotian Shelf by season. A number of models have been developed to describe the dynamics of the Gulf of St. Lawrence and Sable Island herds. All of the models (Mohn and Bowen, 1996; Hammill, 2005; Hammill and Stenson, 2011; Trzcinski et al., 2006; Thomas et al., 2007) fit a population model to pup survey data in the Gulf and on Sable Island, using an initial population size, natural mortality and, in the case of the Sable herd, assumed density dependence on the juvenile age groups. There was a peer review meeting during October 2010 to seek consensus on the grey seal–cod interactions (DFO, 2011) in Atlantic Canada. The parameters used in the grey seal population models developed here are consistent with the consensus derived at that meeting.

The Gulf, Eastern Shore and Sable herd models estimate abundance of males and females for ages 0 (pups) to 39. Age-specific reproductive rates (number of pups born per year by female age) are from Hammill and Stenson (2011). The numbers of pups are based on surveys and mark recapture studies conducted since 1962 (Hammill and Stenson, 2011; 2010 data from Bowen, pers. comm.). The three herds experience mortality due to a variety of human activities including killing of nuisance seals under licence, scientific collections, commercial harvests and culls. Hammill and Stenson (2011) provide a comprehensive description of these data which are used in the models below. In estimating the removals, it is assumed that all ages are vulnerable to mortality by human activities. Commercial harvests and culls are split into age 0 and 1+ individuals, with the age structure of the latter assumed to be that of the age 1–39 population abundance at the time of mortality.

For all three models, the proportions by age and sex ($P_{s,a}$) in the starting year (1960) are based on a stable age distribution generated assuming the input birth rate and natural mortality estimates applied over an 80 year period. For the Gulf herd, a two-parameter model is used (Eq. (1)). The first parameter estimates the total population size in 1960 (N_{1960}), while the second parameter is a multiplier (U) on the age/sex natural mortality. For the latter, the mortality on age 0 (pups) is assumed to be 15 times that on ages 1+, which is initially set to 0.06, consistent with Hammill and Stenson (2011).

This exponential model is then fit to the observed pup production data:

$$\begin{aligned} N_{1960,s,a} &= P_{s,a} * N_{1960} \\ N_{t+1,s,a+1} &= ((N_{t,s,a} * e^{-M_{s,a} * U^{3/4}}) - Removals_{t,s,a}) * e^{-M_{s,a} * U^{3/4}} \quad (1) \\ Pup_{t+1,s,0} &= 0.5 * \sum N_{t,female,a} * R_a \end{aligned}$$

where $N_{1960,s,a}$ is the seal abundance by sex (s) and age (a) at beginning of 1960, $P_{s,a}$ is the proportion of seals by sex (s) and age (a) for a stable age distribution, N_{1960} is the 1960 abundance parameter fit by the model, $N_{t,s,a}$ is the seal abundance by sex (s) and age (a) at beginning of year t , $M_{s,a}$ is the natural mortality by sex (s) and age (a), $Removals_{t,s,a}$ are the sum of the nuisance, science, commercial harvests and culls by sex (s) and age (a) during year t ; note that

all removals are assumed to occur mid-way through the first half of the year, U is the multiplier of natural mortality by sex (s) and age (a) fit by the model, $Pup_{t,s,0}$ is the seal abundance by sex (s) at beginning of year t , $N_{t,female,a}$ is the female seal abundance at age (a) at beginning of year t , and R_a is the input birth rate at age.

For the Sable herd, DFO (2011) presented evidence for declining Sable herd pup and juvenile survival during the recent years. To be consistent with these observations, density dependence is modelled as a theta-logistic function of total population size, for pups (age 0) and juveniles (age 1–9 males and age 1–5 females). An exponential function is used for all the older ages (Eq. (2)):

$$\begin{aligned} N_{1960,s,a} &= P_{s,a} * N_{1960} \\ Juv_{t+1,s,1} &= (((Pup_{t,s,0} * e^{-M_{s,0} * U / 4}) - Removals_{t,s,a}) * \\ & (1 - N_t / K)^\theta) * e^{-M_{s,0} * U^{3/4}} \\ Juv_{t+1,s} &= ((Juv_{t,s,a} * e^{-M_{s,a} * U / 4}) - Removals_{t,s,a}) * \\ & (1 - N_t / K)^\theta) * e^{-M_{s,0} * U^{3/4}} \quad (2) \\ N_{t+1,s,a+1} &= N_{t,s,a} * e^{-M_{s,a} * U} \\ Pup_{t+1,s,0} &= 0.5 * \sum N_{t,female,a} * R_a \end{aligned}$$

where $N_{1960,s,a}$ is the seal abundance by sex (s) and age (a) at beginning of 1960, $P_{s,a}$ is the proportion of seals by sex (s) and age (a) from stable age distribution, N_{1960} is the 1960 abundance parameter fit by the model, $Pup_{t,s,0}$ is the seal abundance by sex (s) at beginning of year t , $Juv_{t+1,s}$ is the juvenile seal abundance by sex (s) at beginning of year t , N_t is the population total abundance in year t , K is the carrying capacity, θ is the degree of population density dependence (assumed 2.4), $N_{t,s,a}$ is the seal abundance by sex (s) and age (a) at beginning of year t , $M_{s,a}$ is the natural mortality by sex (s) and age (a), $Removals_{t,s,a}$ are the sum of the nuisance, science, commercial harvests and culls by sex (s) and age (a) during year t ; note that all removals are assumed to occur mid-way through the first half of the year, U is the multiplier of natural mortality by sex (s) and age (a), Pup_{t+1} is the seal abundance by sex (s) and age (a) at beginning of year $t+1$, $N_{t,female,a}$ is the female seal abundance at age (a) at beginning of year t and R_a is the input birth rate at age.

Harting (2002) argued that θ (which defines the rate of density dependent response) for marine mammals should be around 2.4. This value is used here. A three-parameter model is used. The first parameter represents the total population size in 1960, while the second parameter is a multiplier on the age/sex natural mortality. For the latter, the mortality on age 0 (pups) is assumed to be 3 times that on ages 1+, which is initially set to 0.06, consistent with Hammill and Stenson (2011). The higher mortality of Gulf herd pups (15 times as opposed 3 times age 1+ M) is due to different habitat conditions (i.e. residence on ice for the Gulf herd pups) during this life history stage.

The third parameter is the carrying capacity (K). Contrary to Trzcinski et al. (2006), the latter was estimated without consideration of whether or not the 2007 estimate of pup production fell within the confidence interval of the aerial survey.

The Eastern Shore model is similar to that of the Gulf herd (Eq. (1)). However, it assumes the same adult natural mortality as that determined in the Sable model. The number of pups predicted to be born per year in each model is fitted to the observed pup production, weighted by the inverse of the observation standard error. A one to one sex ratio at birth is assumed.

The trends in pup and total abundance of the three herds during 1960–2020 are shown in Figs. 3 and 4 respectively. For the Gulf herd, the coefficient of variation (CV) on N_{1960} (the parameter of the 1960 population size (11,645)) was 30.8%, and on U (the mortality multiplier (0.97)) was 9.1%. The Sable model fit the pup data very well, with CVs on the three parameters (N_{1960} , U and K) <6%. As observational support for density dependent mortality is weak (DFO, 2011), the carrying capacity for the Sable herd may be underestimated in both models. The Eastern Shore model fit is poor. The

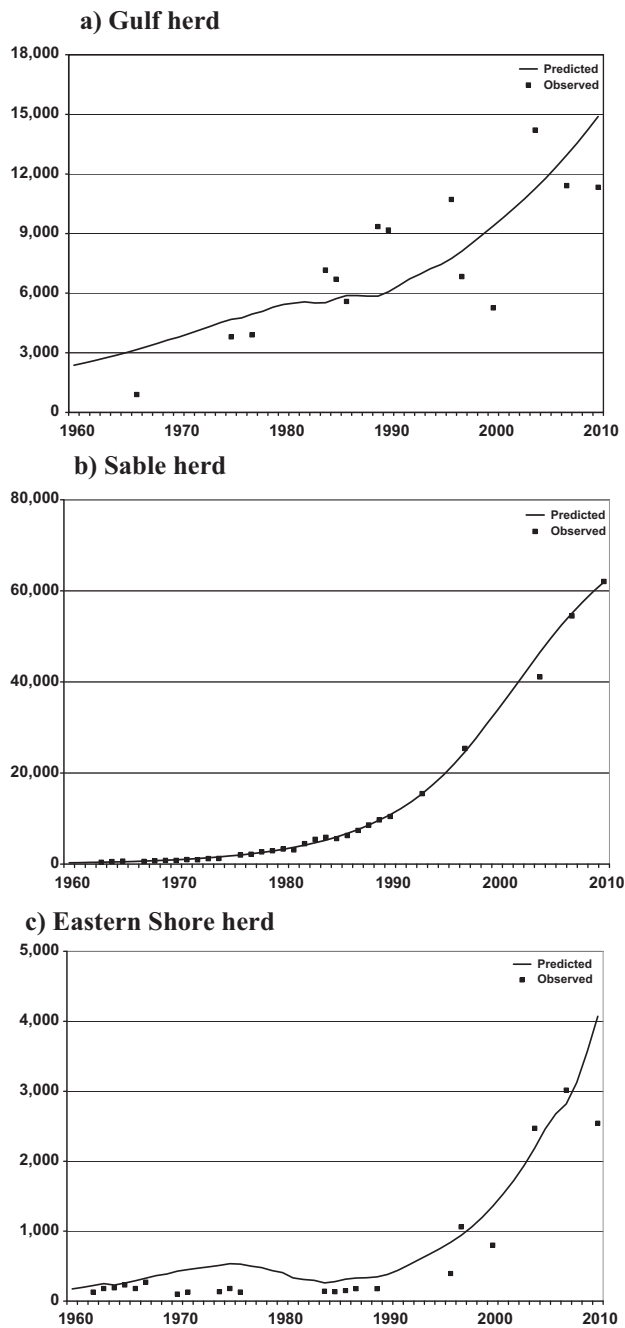


Fig. 3. Trends in observed (dots) and predicted (solid line) pup numbers from the grey seal Gulf (a), Sable (b) and Eastern Shore (c) population models.

CV on the U, the pup multiplier (determined as 3.43) was 137% and there were strong trends in the residuals. The model indicates rapid population growth since the early 1990s. The Eastern Shore population is estimated in 2010 to be relatively small compared to that of Sable (22,250 vs. 317,200).

In summary, the estimates of abundance of the Sable herd during 1970–2009 are relatively precise, whereas the estimates for the other two herds are less certain. The Sable Island herd is about 350,000 individuals, whereas the Gulf and Eastern Shore herds continue to grow exponentially, reaching on aggregate about 200,000 individuals by 2020. Given the much larger size of the Sable herd (compared to the other contiguous herds) during the past three decades, the uncertainty associated with the abundance trends of the Eastern Shore and Gulf herds should have a minor impact on the

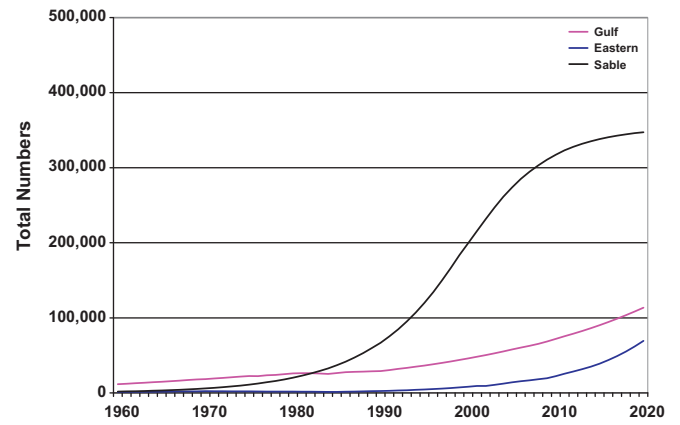


Fig. 4. Gulf, Eastern Shore and Sable grey seal herd total numbers during 1960–2020 as estimated and predicted using the population models.

modelling the seal–cod interactions on the Eastern Scotian Shelf. However, projections to 2020 (and beyond) are highly speculative. The Sable Island herd short-term projection is strongly dependent on the limited density dependent observations during the past few years, while the Gulf and Eastern Shore herd population processes might be expected to change in a density dependent manner at some point in the future. Given these uncertainties, projections on seal–cod interactions beyond 2009 are not considered.

3. Grey seal food consumption

The total consumption of the three seal herds foraging in 4VsW is estimated taking into account the energy requirement of each seal, the energy density of their food, and the abundance of each herd in 4VsW by age, sex, area and season.

The energy requirement (EN in watts) of each male and female seal is based on the Kleiber equation (Mohn and Bowen, 1996; Trzcinski et al., 2006):

$$EN = GP * AF * kW^{0.75} * ME^{-1} \quad (3)$$

As defined by Mohn and Bowen (1996), the growth premium (GP) adjusted metabolic rate decreases geometrically at younger ages such that pups through age five require a premium of 200, 150, 125, 112, 106 and 103% respectively. The activity factor (AF) is assumed to be 2.0 and includes the heat increment. The Kleiber constant (k) is set at 3.4 and the metabolizable energy (ME) at 0.83. Multiplying Eq. (3) by 86.4 converts the watts to kJ per day (i.e. $s * \text{min} * h/1000$). The weights of each seal (W) per day are based upon the consensus agreement arising from the preparatory workshop for the October 2010 workshop (DFO, 2011; H. Benoit, pers. comm.). The energy requirements (EN) of each seal are estimated on a quarterly basis by summing of daily estimates within each quarter. Grey seals of each herd are assumed to fast for the first 20 days of the year (Hammill, pers. comm.; Mansfield and Beck, 1977). The tons consumed per seal in each herd, by quarter, age and sex, are estimated using the quarterly energy requirement divided by the mean energy density (5.74 kJ/g) of the food during 1988–2006 (Mohn and Bowen, 1996; Trzcinski et al., 2006).

To estimate the average abundance of each herd in each NAFO area by quarter, it is necessary to distribute the mortality estimated from the seal population model across quarters. An even distribution (25% per quarter) is assumed except for pups, where 75% of the mortality is assumed to occur in quarters one and two (Trzcinski et al., 2006). The Gulf and Sable grey seal herds undergo extensive migrations on the Atlantic coast as indicated by historical tagging work by Lavigne and Hammill (1993) and recent satellite tagging by Breed et al. (2006, 2009). From these tagging studies, the

Table 1

Proportion of Gulf (a) and Sable (b) herd pup, juvenile and adult male and female population abundance by NAFO area and quarter of year (data provided by M. Hammill and C. den Heyer); pups and juveniles include ages 0–5 and ages 6+ for males and females.

NAFO area	Pups and Juveniles				Males				Females			
	Qtr 1	Qtr 2	Qtr 3	Qtr 4	Qtr 1	Qtr 2	Qtr 3	Qtr 4	Qtr 1	Qtr 2	Qtr 3	Qtr 4
(a) Gulf herd												
3L	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
3PN	0.006	0.003	0.000	0.000	0.031	0.007	0.000	0.000	0.013	0.000	0.000	0.000
3PS	0.047	0.049	0.000	0.000	0.101	0.020	0.000	0.000	0.009	0.000	0.000	0.000
4R	0.010	0.000	0.000	0.010	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
4S	0.000	0.087	0.267	0.178	0.000	0.054	0.121	0.022	0.000	0.121	0.300	0.167
4T	0.112	0.490	0.733	0.655	0.369	0.530	0.851	0.801	0.514	0.444	0.700	0.736
4VN	0.262	0.134	0.000	0.061	0.185	0.104	0.005	0.107	0.060	0.000	0.000	0.051
4VSW	0.499	0.237	0.000	0.096	0.237	0.217	0.023	0.067	0.403	0.429	0.000	0.046
4X	0.008	0.000	0.000	0.000	0.060	0.040	0.000	0.003	0.000	0.006	0.000	0.000
5Y	0.011	0.000	0.000	0.000	0.016	0.029	0.000	0.000	0.000	0.000	0.000	0.000
5Z	0.045	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
(b) Sable herd												
3KL	0.000	0.008	0.000	0.000	0.000	0.000	0.017	0.002	0.000	0.000	0.000	0.000
3PN	0.003	0.000	0.001	0.001	0.000	0.000	0.001	0.000	0.000	0.000	0.000	0.000
3PS	0.022	0.000	0.036	0.029	0.000	0.000	0.004	0.000	0.000	0.015	0.052	0.004
4R	0.001	0.001	0.000	0.000	0.000	0.000	0.007	0.002	0.000	0.000	0.000	0.000
4S	0.003	0.018	0.028	0.042	0.000	0.000	0.040	0.004	0.008	0.047	0.094	0.023
4T	0.056	0.048	0.082	0.059	0.024	0.000	0.048	0.014	0.031	0.067	0.131	0.061
4VH	0.020	0.008	0.020	0.017	0.007	0.002	0.061	0.020	0.046	0.038	0.032	0.004
4VSW	0.846	0.873	0.833	0.852	0.642	0.851	0.792	0.869	0.894	0.833	0.688	0.888
4X	0.031	0.026	0.000	0.000	0.188	0.103	0.031	0.045	0.006	0.000	0.000	0.003
5Y	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
5Z	0.017	0.017	0.000	0.000	0.139	0.043	0.000	0.043	0.000	0.000	0.000	0.000
Missed	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.014	0.000	0.004	0.018

indicates that values set to zero as 4Vn 1st and 4th qtr not part of 4TVn stock.

proportions of pup and age 1+ (male and female) abundance of the two herds by geographic area and season have been estimated (Table 1). Gulf herd seals of all ages generally stay in the Gulf. Sable herd pups stay in 4VsW; while age 1+ males tend to move south, and females tend to move north. The movement of the Eastern Shore Nova Scotia herd was assumed the same as that of the Sable herd. These estimates of spatial distribution of grey seals were used to allocate the quarterly abundance by herd amongst geographic areas, which were then multiplied by the per-capita seal consumption in order to provide estimates of total consumption by herd and area.

It is noted that the spatial distribution of seals from the three herds is assumed here to be constant over time (irrespective of seal herd abundance), and that the estimates of distribution (Table 1) are based on tagging of a relatively small number (229 seals tagged between 1994 and 2009) of individuals (when compared to the population abundance). However, most of the tagging has been undertaken in recent years during a period of high abundance of the Sable herd. Also, it is probable that seals forage over a broader geographic area as abundance has increased. Thus, the geographic patterns summarized in Table 1 are more reflective of seal distribution at high population abundance. At lower abundance, it is to be expected that a higher proportion of the Sable herd forages on the Eastern Scotian Shelf. This implies that the application of the proportions shown in Table 1 throughout the 1970–2009 period underestimates seal food consumption in 4VsW during the earlier decades. The direction of this bias is to be noted in the discussion of the results of the seal–cod interaction model.

The estimates of annual food consumption on the Eastern Scotian Shelf by grey seals in the three herds are shown in Fig. 5. While the Gulf herd is estimated to have consumed 138,000 t in 2010, only 17,000 t of this is from 4VsW. In contrast, the Sable and Eastern Shore herds combined are estimated to have consumed 556,000 t in 2010, 346,000 t of this in 4VsW. The interactions between grey seals and 4VsW cod are dominated by the Sable and Eastern Shore herds.

4. Functional response of seal predation on cod

4.1. Literature review

There is an extensive literature on the food habits of grey seals off Atlantic Canada and Europe (including Iceland). The diet composition information for seals in the northwest Atlantic covers the time period from 1950 (Fisher and Mackenzie, 1955) to 2010 (Hammill et al., 2007; Bowen and Harrison, 2007; Bowen et al., 2011; Stenson et al., 2010). For the northeast Atlantic, there are published observations from 1967 (Rae, 1968, 1973) to 2002 (Hammond and Harris, 2006; Hammond and Grellier, 2006). During these several decades, the relative abundance of the diverse grey seal and Atlantic cod populations has varied considerably. Also, there are differences between studies in the methods used to estimate the diet.

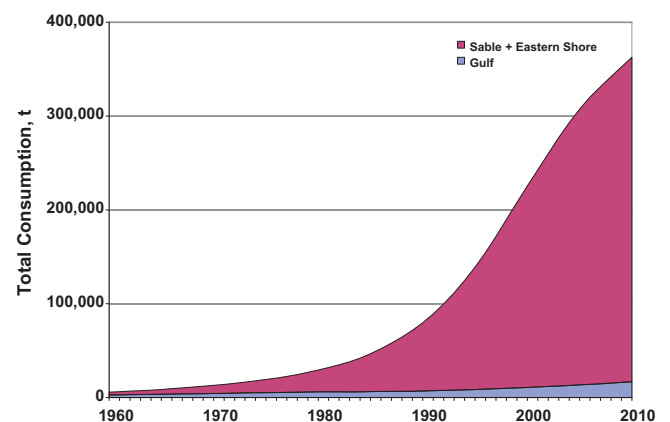


Fig. 5. Estimates of total food consumption by the Gulf, Eastern Shore and Sable grey seal herds within 4VsW.

Three methods have been used to estimate the species composition of the diet: (1) analysis of stomach contents of seals that have been killed (e.g. Hammill et al., 2007), (2) analysis of scat at sites where seals have defecated on land (see Grellier and Hammond, 2005, 2006; Bowen et al., 2011 for recent evaluations of the method), and (3) analysis of fatty acids in the blubber of seals (Iverson et al., 2004). Each method has strengths and weaknesses. The “stomach analysis” method is constrained by the relatively small number of samples that can be collected due to the intrusive nature of the sampling (killing seals). The digestion process masks precise identification of relative abundance of items in the diet, and the stomach contents only reflect recent feeding activity (about 24 h). The “scat analysis” method also reflects recent feeding, as well as foraging activity close to land. As the diet is reconstructed from hard parts (otoliths for fish species), it is assumed that seals consume the head of most prey items. The “fatty acid analysis” method has the potential advantages that foraging activity over several weeks to months can be estimated, the sampling is relatively unobtrusive, and the feeding activity can be sampled throughout the distributional range of the species. The weaknesses are that the composition of ingested lipids can be modified by seals during metabolism, new synthesis, and utilization. The fatty acid composition differences between species in the diet need to be large to leave diagnostic patterns in the blubber. The fatty acid signature can be for taxonomic groups rather than being species specific, and prey lipid composition varies with physiological state and seasonal cycles. Experimental support is limited (Nordstrom et al., 2008), and the application of the method to estimate quantitative diet composition of marine mammals has not been without controversy (see Grahl-Nielsen et al., 2003, 2004; Thiemann et al., 2004 for exchange of perspectives). Grahl-Nielsen et al. (2011) conclude that the “fatty acid analysis” method cannot be used for quantitative estimates of seal diets.

The estimates of the relative species compositions are generally expressed in two ways, percent frequency and percent weight (or mass). For the purposes of estimating annual consumption of diverse species (in this case cod) by the grey seal populations, the latter estimate is preferable. A synopsis of the global literature on the proportion of Atlantic cod in the diet of grey seals is provided in Table 2. Although there is considerable variability (seasonally, geographically, and over the several decades of sampling), cod is a significant component of the diet of grey seals in all areas and at all times (when the “stomach analysis” and “scat analysis” methods are used). It is frequently amongst the top five diet items.

In the northwest Atlantic, sampling has covered the coastal areas from Cape Cod to Newfoundland with the most extensive work done on Sable Island. The notable outlier is the average of the results using the “fatty acid analysis” method on Sable Island (1993–2000). There is a period of overlap (1993–1998) when both the “scat analysis” and “fatty analysis” methods were used to estimate diet composition on grey seals sampled in this area. The “scat analysis” method overall estimate for Sable Island samples is 13.3% (unadjusted for otolith dissolution) and 7.1% (adjusted for otolith dissolution) by weight based on 920 samples, whereas the “fatty acid analysis” method estimate is about 1% by weight based on 496 samples. The global average (i.e. for grey seal diets throughout the distributional range of the species) is about 10–15% cod in the diet. Tollit et al. (2009), using DNA techniques, conclude that the traditional scat method is doing a reasonable job in identifying major diet components of pinnipeds.

The global literature (as summarized in Table 2) suggests that cod continues to be a major component of grey seal diets even during periods of extremely low cod abundance. This is evident in 4VsW. During 1991–1998, when the cod population complex on the Eastern Scotian Shelf is estimated to have been in a collapsed state, the percentage of cod in the diet of seals feeding in the vicinity

of Sable Island was 7.1% by weight. Hammill et al. (2007) make the same point for the Southern Gulf of St. Lawrence, but note that the proportion of cod in the diet of grey seals feeding along the west coast of Newfoundland declined as cod abundance declined. A recent study (2008) in the Cabot Strait indicates that the % cod in the diet is 46% by weight (Stenson et al., 2010), in spite of the very low abundance of cod.

These observations suggest that the proportion of Atlantic cod in the diet of grey seals is weakly related to cod abundance (at least over the broad range of abundances for which there have been samples). As indicated by the fishing industry, grey seals may seek out aggregations of prey, in a manner similar to purse seiners seeking out schools of herring. As such, the proportion of cod in the diet may be relatively constant and independent of the abundance of cod over a wide range of prey stock sizes. Hammill et al. (2007) draw a similar conclusion. It is, however, recognized that at some level of cod abundance, the assumption of a constant proportion of cod in the diet is unrealistic. If this were true, seals would ‘run out’ of cod in the early 2000s when abundance of this prey was low. The nature of the density dependent “functional response” of grey seals to changes in abundance of prey species is explored in the next section.

4.2. Cod–seal functional response

It is to be expected that the percent cod by weight in a seal’s diet is some function of cod abundance. Mohn and Bowen (1996) assumed both constant and proportional (to cod biomass) functions. Trzcinski et al. (2006) developed a “Holling type II” predator–prey functional relationship for the pups and juveniles, but not the adults. A similar type II predator–prey relationship (Eq. (4)) was used here, which describes annual percent weight of cod in grey seal diet as a hyperbolic function of total cod population biomass. This differs from that of Trzcinski et al. (2006) in that cod biomass rather than numbers is modelled:

$$P_t = \frac{q * B_t}{1 + (q * B_t)/P_{MAX}} \quad (4)$$

where P_t is the percent weight (tons) of cod in grey seal diet in year t , P_{MAX} is the maximum annual percent weight (tons) of cod in grey seal diet, q is the coefficient of interaction between cod and grey seals and B_t is the mean total cod biomass in year t .

The range in the estimates of percent cod in the diet throughout the distributional of grey seals is shown in Table 2. Although there are some extreme observations as high as 40%, the aggregate observations infer a maximum in the range of 20–25%. A P_{MAX} value of 22% is used here, being consistent with these observations and the value used by Trzcinski et al. (2006). For given values of P_t , B_t and P_{MAX} , the coefficient of interaction, q , can be iteratively estimated as:

$$q = P_t \left(\frac{1}{B_t} + \frac{q}{P_{MAX}} \right) \quad (5)$$

Observations on percent cod in grey seal diet for Sable Island are available during 1991–1998 (Table 2), a time period of relatively low cod abundance. These range from <1 to 13% with a mean of 7%. To explore the sensitivity of the seal–cod interaction to estimates of q , P_t values of 3.5, 7 and 12% were chosen to solve Eq. (5) using estimates of mean 1991–1998 B_t from the cod population model (see below).

To illustrate the above type II cod–seal functional relationship, B_t estimates for 1991–1998 from the annual summer bottom trawl survey, along with P_{MAX} of 22% and P_t values of 3.5, 7 and 12% were used to estimate q for each of three functional models (Fig. 6). As P_t increases towards P_{MAX} the relationship becomes increasingly hyperbolic. The three scenarios illustrated in Fig. 6 of

Table 2
Summary of global literature on percent cod in grey seal diet.

Country	Years	Method	Percent wt	Rank in diet	# Samples	Reference
Iceland	1979–1982	Stomach	22.0	1	97	Hauksson (1985)
Iceland	1992–1993	Stomach	25.1	1	737	Hauksson and Bogason (1997)
British Seas East coast	1983–1988	Scat	21.6	2	236	Hammond and Grellier (2006)
British Seas Orkney	1985	Scat	5.1	2	859	Hammond and Grellier (2006)
British Seas Donna Nook	1985	Scat	12.1	2	360	Hammond and Grellier (2006)
British Seas East coast	2002	Scat	8.2		429	Hammond and Grellier (2006)
British Seas Orkney	2002	Scat	10.2		711	Hammond and Grellier (2006)
British Seas Shetland	2002	Scat	7.7		244	Hammond and Grellier (2006)
British Seas Donna Nook	2002	Scat	4.5		429	Hammond and Grellier (2006)
British Seas Aggregate	2002	Scat	8.0	2	1740	Hammond and Grellier (2006)
Gulf of St. Lawrence upper	1950–1987	Stomach	22.8 (freq)	2	316	Benoit and Bowen (1990a)
Gulf of St. Lawrence lower	1950–1987	Stomach	13.5 (freq)	4	89	Benoit and Bowen (1990a)
Gulf of St. Lawrence, Newfoundland inshore	1985–2004	Stomach	4.2	4	25	Hammill et al. (2007)
Gulf of St. Lawrence Anticosti Island	1988–1992	Stomach	17.8	5 (spring) 1 (fall)	183	Hammill et al. (2007)
Gulf of St. Lawrence lower	1994–2003	Stomach	12.8	4	322	Hammill et al. (2007)
Gulf of St. Lawrence Cabot Strait	2008	Stomach	46.5 (energy)	1 (males)	50	Stenson et al. (2010)
Scotian Shelf coastal	1950–1987	Stomach	13.6 (freq)	3	213	Benoit and Bowen (1990a)
Scotian Shelf Sable Island	1950–1987	Stomach	21.3	1	47	Benoit and Bowen (1990a)
Atlantic Canada Aggregate	1950–1987	Stomach	18.5	1	682	Benoit and Bowen (1990a)
Scotian Shelf Inshore	1988–1990	Stomach	17.0	2	106	Bowen et al. (1993)
Scotian Shelf Sable Island	1988–1990	Stomach	10.3	5 (summer) 2 (winter)	37	Bowen et al. (1993)
Scotian Shelf Sable Island	1991–1998	Scat	7.0	3	1304	Bowen and Harrison (2007) and Bowen et al. (2011)
Scotian Shelf Sable Island	1993–2001	Fatty Acid	1.9	>10	587	Beck et al. (2007)
Gulf of Maine	2004–2008	Scat	6.4	3	305	Ampela (2009)
Gulf of Maine	1998–2004	Stomach	1.7	8	49	Ampela (2009)

the predator–prey functional relationship are used to explore the seal–cod interactions in the cod population model.

5. Size and age selectivity of cod in grey seal diet

Most of the studies on the food habits of grey seals provide estimates of the size composition of the major prey items. Although the literature indicates that grey seals consume predominantly small cod (with the size composition varying between locations

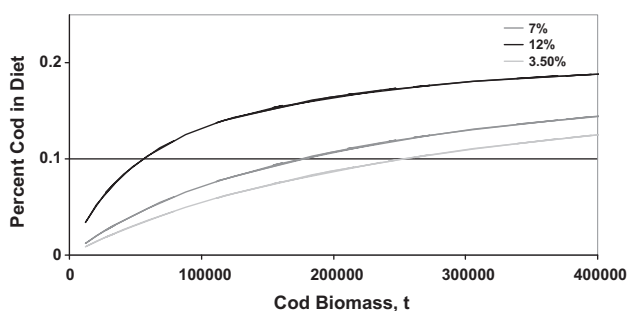


Fig. 6. Type II cod–seal functional relationship for three (3.5, 7 and 12%) assumptions of percent cod in grey seal diet during 1991–1998; P_{MAX} assumed equal to 22%.

and years, Table 3), it is uncertain whether they are selecting for smaller cod or rather just consuming what is available. Small cod are more abundant than older cod, thus one would expect to see mainly small cod in the diet, in particular for seal stomachs and scat sampled at locations such as Sable Island which are close to juvenile cod nursery areas (Gagne and O'Boyle, 1984). These points are illustrated in Fig. 7, which considers research vessel trawl survey data from the 1980s. The size composition of cod in survey strata close to Sable Island (area representative of the scat samples for which the size and age composition of the seal diets have been derived), is composed of somewhat smaller cod compared to 4VsW as a whole. Thus, feeding by seals in the vicinity of Sable Island may not represent the size composition of the diet in the overall Eastern Scotian Shelf area.

Mohn and Bowen (1996) and Trzcinski et al. (2006, 2009) partition the estimated total cod consumed into age classes based on the percent at age observed in the aggregate scat samples from Sable Island. They do not relate the length frequencies from the scat samples to the length frequencies of the cod available in the area around the island, nor evaluate the degree to which seals are feeding on the size range that is available. This approach (based on Sable Island scat samples) provides a somewhat biased estimate of the size composition of cod eaten by grey seals throughout the 4VsW stock area. An additional point from Fig. 7 is that very few

Table 3
Summary of the literature on the size range of cod in the diet of grey seals.

Location	Length range (cm)	Mean (cm)	Reference
North Sea (1983–1988)	10–75	40	P. Hammond, pers. comm.
North Sea (2002)	10–80	38	P. Hammond, pers. comm.
West of Scotland (1985)	15–70	40	P. Hammond, pers. comm.
West of Scotland (2002)	20–75	44	P. Hammond, pers. comm.
Anticosti Island (1982–1987)	10–75	28	Benoit and Bowen (1990b)
Northern Gulf of St. Lawrence (1985–2004)	5–65	38	Hammill et al. (2007)
Southern Gulf (1985–2004)	5–65	28	Hammill et al. (2007)
Newfoundland (east coast) (1985–2004)	5–65	32	Hammill et al. (2007)
Scotian Shelf (1988–1993)	10–48	25	Bowen et al. (1993) and Bowen and Harrison (1994)
Southern Gulf (2008)	10–70	43	Stenson et al. (2010)

larger cod are observed in the 4VsW management area, even during the 1980s which was a period of relatively high abundance and lower mortality rates. Thus, large cod in the diet are expected to be rare, even if seals were feeding in a non-selective manner.

Bowen and Harrison (1994), based on a comparative analysis of the size composition of prey species in the feeding area around Sable Island (using observations from research vessel trawl surveys) and the size composition in the diet, concluded that grey seals do not select for particular size classes of Atlantic cod, American plaice, and Yellowtail flounder, but rather consume what is available. Stenson et al. (2010) observed predominantly large cod in the stomachs of grey seals sampled in the Cabot Strait cod overwintering area (2008 winter study). Beck et al. (2007), using the “fatty acid analysis” method, report that grey seals on the Scotian Shelf preferentially consume cod >35 cm.

An additional complication in drawing conclusions on the degree to which grey seals may avoid larger cod is the observation by fishermen that the heads of the larger fish are not consumed (and thus the otoliths of larger cod are under-represented in the stomach and scat samples). The counter to these observations has been that these cod were consumed while stuck in gillnets. However, the anecdotal reports are also from observations not involving fishing gear.

In summary, the literature provides contradictory observations with respect to the size selectivity of cod consumed by grey seals. Due to this uncertainty two scenarios are explored in modelling the size selection of cod during seal feeding. Given the relatively small sample size for estimation of size composition of the diet components (and the observed variability), the constraint that the “stomach analysis” and “scat analysis” methods predominantly

track feeding in the coastal zone (within which juvenile cod tend to be more prevalent), and the unknown prevalence of “belly-biting” (i.e. not consuming the head of larger cod), one approach is to assume that grey seals consume the size classes of cod that are available (above a certain minimum size). In modelling the impact of seal predation on cod, this behaviour is estimated using a “flat-top” partial recruitment (i.e. selectivity pattern at age) vector (Fig. 8). For age one, the assumed partial recruitment of cod to seals is 0.5, consistent with the earlier models of Mohn and Bowen (1996) and Trzcinski et al. (2006). For all older ages, the partial recruitment was assumed equal to one. A second approach is to use a dome shaped partial recruitment vector for the “seal fleet” (Fig. 8). This relationship was estimated through an analysis of the cod mortality at age due to seals, from the population model of Mohn and Bowen (1996).

6. Role of seals in natural mortality of cod

The previous sections summarize available information on the fraction of cod, and the size selectivity, in grey seal diets. In the cod population model described below, these two uncertainties are explored through a combination of scenarios for selectivity (flat top and domed partial recruitment illustrated in Fig. 8), and functional responses (illustrated in Fig. 6). The latter scenarios on diverse functional relationships generate estimates of annual percent weight of cod in grey seal diet during 1970–2003.

6.1. Modelling approach

The ADAPT formulation of cohort analysis (Gavaris, 1988) was used to estimate cod population trends and mortality due to fishing, seals, and other sources.

The catches at age (ages 1–15) from the fishery are for 1970–2009.

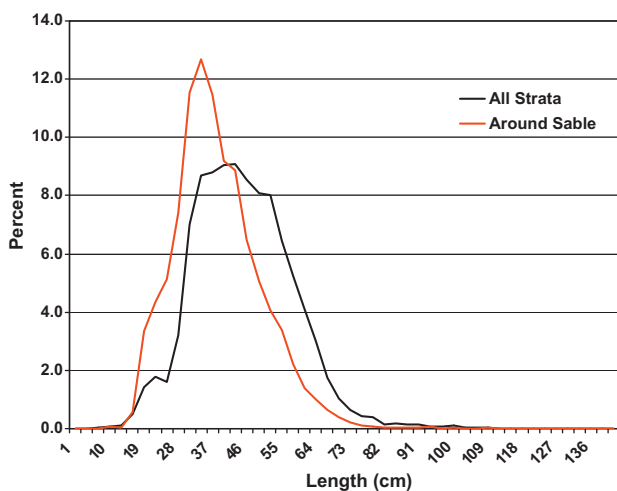


Fig. 7. Average 1980–1989 percent length (cm) composition of cod encountered in DFO summer survey strata in the vicinity of Sable Island, where cod juveniles are known to aggregate, and all strata in 4VsW.

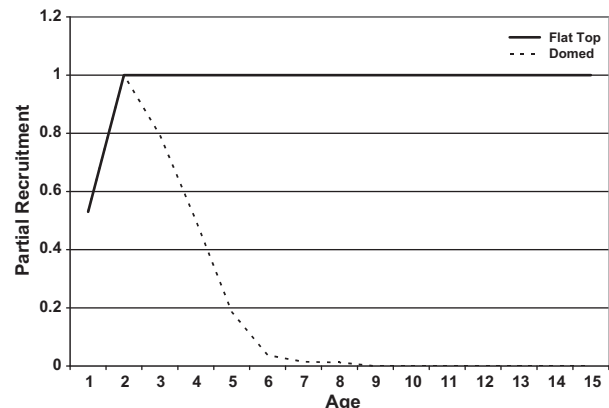


Fig. 8. Partial recruitment assumptions used in cod–grey seal interaction model.

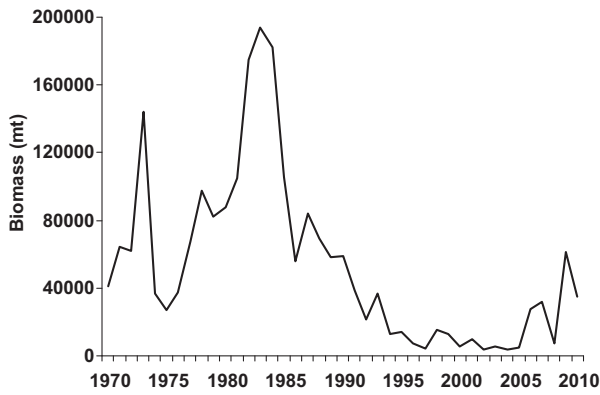


Fig. 9. Trend in 4VsW cod total mid-year biomass based upon DFO summer bottom trawl survey.

Cod biomass consumed by seals is estimated from the total seal consumption multiplied by the proportion of cod in the diet from the type II model. An issue was encountered during preliminary runs of the model. Since 2003, the total cod biomass is estimated from the trawl surveys to have significantly increased (Fig. 9). The functional relationships estimated high cod consumption by seals that could not be accommodated by the model. A heuristic approach was used to address this problem, with a linear increase in percent cod in grey seal diet, from 1.5 to 3.5%, assumed for the 2004 to 2009 years (3.5% is the 2010 estimate from analysis of scat on Sable Island, Bowen et al. (2011)).

The method for estimating the mortality due to seals is outlined in Appendix A and used the survey weights at age as representative of the weight of cod in the seal diet.

M_{other} (natural mortality due to predators other than seals) is estimated as a random walk (Eq. (6)) using eight time blocks of three year duration (1986/1988–2007/2009):

$$M_{other,b+1} = M_{other,b} * e^{dev} \tag{6}$$

where $M_{other,b}$ is the M_{other} in time block b and dev is estimated deviation in M_{other} .

Preliminary explorations of time blocks of 1–4 years duration indicated that a three year time block provided more stable results across the selectivity–diet scenarios that are modelled. These runs also indicated that while the precise trends in M_{other} were sensitive to block size, the overall trends were the same (Fig. 10). M_{other} was assumed to be equal for all ages, as preliminary runs indicated that there is not enough information in the data to determine M_{other} trends by age. Prior to 1986, M_{other} was assumed equal to 0.2.

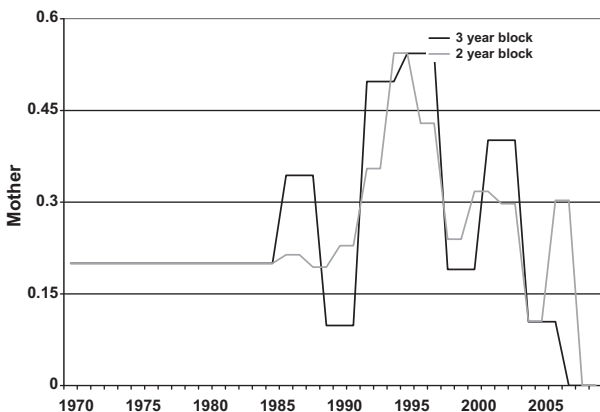


Fig. 10. Estimates of M_{other} using time blocks of two and three year duration; flat top selectivity and 7% diet assumed.

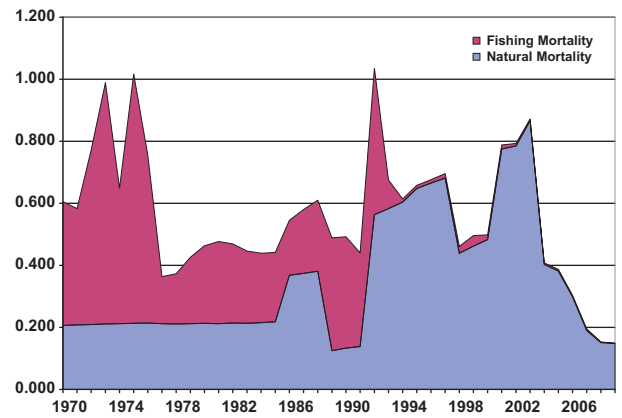


Fig. 11. Trends in age 5–7 4VsW cod mortality due to fishing and natural mortality from ADAPT model assuming flat top selectivity and 7% cod in grey seal diet.

The parameters calibrated are the 2009 ages 2–15, and the 1985–2009 age 15 beginning of year cod numbers at age, and M_{other} for each of eight time blocks (1986/1988–2007/2009). Age 15 beginning of year cod numbers at age for 1970–1984 are estimated assuming fishing mortality as the average on ages 4–6.

The summer research trawl survey observations are used in the minimization of the objective function (Eq. (7)). Log observation error is assumed:

$$\Phi = \sum_{a,t} (\ln I_{a,t} - (k_a + \ln N_{a,t}))^2 \tag{7}$$

where $I_{a,t}$ is the age 1–8 summer bottom trawl annual mean numbers per tow for 1970–2009, k_a is the age 1–8 calibration coefficient; the algorithm estimates this analytically (Gavaris, pers. comm.), and $N_{a,t}$ is the age 1–8 population numbers from the ADAPT model for 1970–2009, adjusted to mid-year.

The ADAPT model consists of 47 parameters with 320 observations. The mean square residual (MSR) was used as the criterion for model selection. All modelling is undertaken in the J programming language (<http://http://www.jsoftware.com/index.html>).

6.2. Results of cod population modelling

The MSR of each of the six scenarios on combinations of selectivity and % cod in the seal diet indicate that the best overall model fits were obtained using the flat top selectivity model. With respect to selectivity, the fit of the flat top runs marginally decreased with increasing diet percentage, while the opposite is the case for the domed selectivity runs. The differences across diet were less than across selectivity. That said, the differences in MSR across all combinations are small.

	3.5%	7%	12%
Flat top	0.5527	0.5514	0.5495
Dome	0.5787	0.5868	0.6050

The uncertainties in the estimated parameters for the flat top/“7%” functional response scenario are provided in Appendix B. They indicate that while the ages 1–14 numbers at age for 2009, and those at age 15 for 1985–2009, are reasonably well estimated, M_{other} is not (particularly in recent years). This highlights the difficulty in estimating the impact of seals in relation to other sources of M.

The results of the ADAPT model assuming a flat top selectivity and the intermediate functional relationship are illustrated in Fig. 11. Prior to the closure of the fishery in 1993, much of the total mortality was due to fishing. However, natural mortality is estimated to have increased in the mid 1980s, levelling off in the mid-1990s. It is estimated to have remained

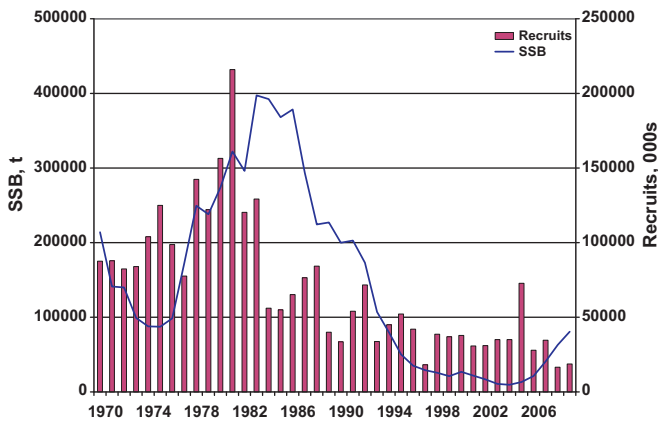


Fig. 12. Trends in spawning stock biomass (age 3+) and recruitment (age 1) of 4VsW cod, based upon flat top, 7% ADAPT model.

high until mid-2000s after which it declined to levels comparable to those estimated prior to the 1980s. Regardless of the “selectivity–functional response scenario”, this general pattern was evident.

Strong recruitment to the stock during the late 1970s contributed to the rise in spawning stock biomass (SSB) in the 1980s (Fig. 12). Recruitment declined in the mid 1980s and has been relatively stable since the mid-1990s. The combination of lower recruitment and increasing total mortality (due to fishing and natural causes) contributed to the rapid decline in SSB prior to the 1993 fishery closure. The recent increase in SSB since 2004 is due to a combination of a relatively strong 2004 year-class and the recent decline in overall natural mortality.

The source of increased natural mortality subsequent to the closure of the fishery in 1993 is not unreported catch. Gavaris et al. (2010) estimated the level of by-catch and discards of cod by fisheries in the 4VsW area during a representative period of the fisheries closure. The average annual estimate from all fisheries sources is <5 t annually. In contrast, annual cod biomass lost due to natural mortality is estimated to have ranged from about 60,000 t in 1993 to about 6000 t in 2004.

Trends in M_{other} under different assumptions of percent cod in grey seal diet (i.e. different functional relationships) for the flat top selectivity are provided in Fig. 13. As percent cod in grey seal diet increases, M_{other} significantly declines, particularly since the mid-1990s, implying that seals make up an increasing portion of natural mortality during this period. This is illustrated in Fig. 14, which shows the cod biomass consumed by seals as a percent of biomass

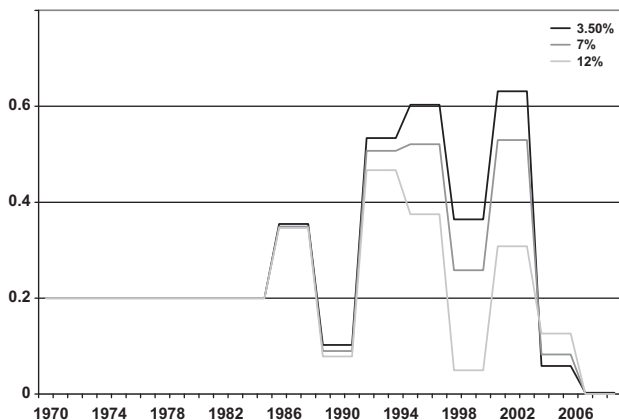


Fig. 13. Trend in M_{other} from ADAPT models assuming P_{MAX} of 22% and a flat top selectivity.

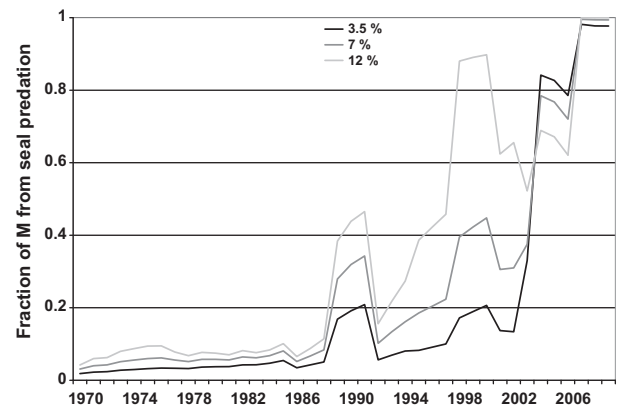


Fig. 14. Percent of natural mortality accounted for by seal predation for three scenarios of type II functional response, assuming flat top selectivity.

lost through natural mortality. Using seal dietary values which are consistent with the literature (Table 2) and a flat top selectivity, type II functional responses can be defined which accounts for a large percentage of the unaccounted M_{other} since the mid-1990s. All scenarios indicate that essentially all natural mortality in recent years is due to seals. Similar trends are observed when a domed selectivity is assumed (Fig. 15). However, in this case, less of the unaccounted M_{other} can be attributed to seal predation.

7. Discussion

There are several uncertainties that are important to consider prior to drawing conclusions on the model results outlined above.

Seal abundance trends during the past five decades are well described for the Sable herd, but are less precise for the Gulf and Eastern Shore herds. It appears that the exponential phase of growth for the Sable herd may be close to over, and that some stabilization may occur in the near future. It is to be expected that exponential growth will continue for some time for the other herds, and possibly new “pupping” areas occupied. Given these uncertainties future projections on grey seal abundance (from the three herds) on the Eastern Scotian Shelf are highly speculative.

The seasonal and spatial distributions of Grey seals from the several herds during 1970–2009, and the changes in distribution that have resulted from abundance increases and shifts in distribution of prey items, are not well understood. In general terms, the expansion in range has been tracked by the fishing industry, and the relatively recent use of satellite tags is providing valuable information on seasonal migrations and on foraging behaviour (Breed et al., 2009). To

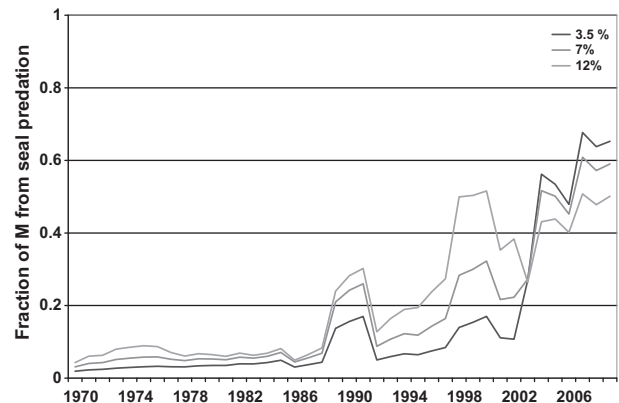


Fig. 15. Percent of natural mortality accounted for by seal predation for three scenarios of type II functional response, assuming domed selectivity.

date, only about 229 seals have been tagged in this manner, mostly from seals on Sable Island. In this study, the spatial distributions garnered from the tagging results during the past decade (Table 1) are considered to represent past distributions over four decades. Also, the spatial distributions of the coastal Nova Scotia and Gulf of Maine herds have not been considered. Given that most of the tags have been on Sable herd individuals, and that the seals from this herd are by far the majority on the Eastern Scotian Shelf during 1970–2009, the application of a static view of foraging is considered to be reasonable for the past two decades, but probably underestimates the proportion of the Sable herd staying within the Eastern Scotian Shelf area during the 1970s and 1980s. If this interpretation is valid, seal predation on cod during the 1980s would be expected to be higher than estimated in the cod population model.

Perhaps the most difficult challenge in evaluating seal/cod feeding dynamics is characterizing the parameters of the functional response of seal foraging. During the past several decades, cod fluctuated at relatively high levels of abundance from 1970 to the early 1980s and then declined monotonically to 2005, followed by a recent upswing (Figs. 9 and 12). The empirical observations on seal diets (summarized in Table 2), as well as the observations from the fishing industry and the tagging studies, indicate several general points. Grey seals are opportunistic foragers with eclectic tastes. Cod is a major diet item of grey seals throughout their distributional range, from the Gulf of Maine to the North Sea. Even when cod abundance is low, they are an important item in the diet. These observations imply that there is an increase in “catchability” as the prey abundance declines. The aggregate number of diet samples is relatively small, and the data highly variable (with a mean value of about 10–15% by weight of cod in the diet during periods of moderate cod abundance). At some level of prey abundance, this proportion must decline. Three scenarios are developed for the type II functional response. It is noted that other studies have come to different conclusions on the nature of the functional response. These studies have relied predominantly on the diet studies using the QFASA method and, in our view, have under-estimated the impacts of seal predation on cod population trends. The recent detailed study by Grahl-Nielsen et al. (2011) supports this perspective (i.e. the lack of utility of the “fatty acid analysis”, or QFASA, method).

The final critical assumption considered in this paper is the degree to which grey seals avoid eating larger and older cod. The empirical observations are contradictory and difficult to interpret. The scat collections from Sable Island are biased towards smaller cod, as the feeding area in the vicinity of the island is a juvenile nursery area and thus not representative of the overall feeding area of 4VsW (Fig. 7). Furthermore, the fishing industry reports multiple observations of “belly biting” of larger cod, even in the absence of fishing gear. If this feeding behaviour is prevalent, the scat (and stomach) samples are further biased towards smaller cod. Models which use the scat samples solely from Sable Island to describe age-specific seal predation will likely be biased. The degree to which seals are actually selecting size classes from the feeding area has generally not been considered. Recent observations from the Cabot Strait cod overwintering area indicate that grey seals do not avoid larger cod, but rather prey on what is available (Stenson et al., 2010). The approach taken in this study is to treat the seal herd as an additional fishing gear sector with its own partial recruitment vector (two scenarios were used to bracket the diverse observations on size selectivity of seals feeding on cod).

In summary, there are several critical uncertainties about key parameters in the models, assumptions about which influence the results to a considerable degree. In this study, the choice of assumptions leads to results that are contrary to other studies that have addressed seal/cod interactions on the Eastern Scotian Shelf. We conclude that grey seals could well be a primary source of

unaccounted for natural mortality subsequent to the 1993 fishery closure. It is also concluded that the increase in natural mortality since the 1990s due to grey seal predation has been an important contributor to the lack of recovery of the stock. However, as noted above, the functional model over-estimates seal consumption of cod in recent years.

There is a tacit assumption that cod and seals have co-existed for centuries in a predator–prey balance, within which cod natural mortality has been sustained at moderate levels (at about 20% annual losses for ages 2 and older). However, it may well be that this ecosystem has been in a state of flux during the past several centuries. It is of interest to trace the historical trends in abundance and distribution of grey seals and cod, in at least a qualitative manner. There is considerable evidence that cod were very abundant within the present distributional area of grey seals during the 19th century (Rosenberg et al., 2005). The evidence is less clear for grey seals. Wood et al. (2007) provide evidence that the southern limit of distribution of this species during the 1800s up until the 1970s was coastal Nova Scotia (and presumably the coastal area of New Brunswick in the Bay of Fundy and approaches). Grey seals were not observed within the Gulf of Maine and Cape Cod until recent decades. From a distributional perspective, the present range has not been experienced since at least the early 19th century.

There is limited quantitative information on abundance of grey seals in the northwest Atlantic prior to the 1960s. Given the seasonal migrations of the Sable Island herd, which includes aggregations of adults on the island from late December to mid-February for pupping, the winter observations are a potential qualitative barometer of abundance trends. In recent years, in excess of 100,000 adult seals “haul out” on the island, with on the order of 50,000 pups being born. Given the financial opportunities alone, one would expect that winter residents during the era of explorations of North America would have remarked on such an interesting natural history phenomena, if it had indeed occurred. The first humans on the island during the winter months (with the possible caveat of survivors of shipwrecks) were the participants of the de la Roche expedition of 1599–1601 (Lanctot, 1933). They would have had the opportunity to observe the winter migrations. The lack of documentation on such an event suggests that abundance levels were lower at that time. Desbarres overwintered on the island in the mid-1700s, and notes that in a pond there were “prodigious numbers of seals” (Morse, 1935). However, the winter aggregation for pupping was not recorded. In 1802, a small community of 35–40 people was established on the island to help the survivors of shipwrecks. The superintendent counted seals and notes that “seals innumerable are basking on the warm sands” (Gilpin, 1858, p. 11). The pupping activity in mid-winter is noted, but no counts are available. Gilpin (1869) notes that the numbers of grey seals were low compared to earlier times (several hundred during the mid-winter months). In summary, present levels of grey seal abundance have not been observed on Sable Island since at least the mid 1800s.

It is concluded that the increases in natural mortality of cod on the Eastern Scotian Shelf since the late 1980s have been due in a large part to the exponential growth of the grey seal population. The assumptions made in this study (and the associated model results) are, however, inconsistent with the estimated recent increase in cod abundance (i.e. since 2005). This could be due to several reasons. The model assumptions may be unrealistic, the estimated recent upswing in the cod abundance may be overestimated in the bottom trawl surveys, and/or there may be a lag in the response of the seals to an increase in prey. Frank et al. (2011) interpret the recent increases in the abundance of cod on the Eastern Scotian Shelf as being part of a shift in ecosystem structure due to a reduction in pelagic fish abundance and associated trophic level interactions. They do not consider that seal predation has played

an important role, neither in the cod population temporal trends nor in the estimated fluctuations in natural mortality. The coming years will hopefully provide observations that clarify the diverse interpretations.

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Appendix A. Estimation of natural mortality due to seals

The estimation of M_s (natural mortality due to seals) in the ADAPT model was undertaken analogous to the determination of the fully recruited fishing mortality, given a fishery quota (in this case, the total cod consumption by seals).

In a given time period (i.e. year), the population average natural mortality due to seals is:

$$M_{s,mean} = \frac{\sum M_{s,a} * B_{c,a}}{\sum B_{c,a}} = \frac{M_s * \sum PR_a * B_{c,a}}{\sum B_{c,a}} \tag{A.1}$$

where $M_{s,a}$ is the natural mortality at age due to seals, M_s is the fully recruited natural mortality due to seals, $B_{c,a}$ is the mean cod biomass at age a equal to $W_a * N_a * (1 - \exp(-Z_a))/Z_a$, W_a is the weight at age a from the DFO summer survey, N_a is the beginning of year cod numbers at age a , Z_a is the total mortality at age a equal to $F_a + M_s * PR_a + M_{other,a}$, F_a is the fishing mortality at age, $M_{other,a}$ is the natural mortality at age due to non-seals, and PR_a is the partial recruitment at age a due to seals.

Now

$$M_{s,mean} = \frac{Seal\ Diet}{\sum B_{c,a}} \tag{A.2}$$

where *Seal Diet* is the biomass of cod consumed by the seal herds.

Therefore, equating (A.1) and (A.2):

$$\frac{M_s * \sum PR_a * B_{c,a}}{\sum B_{c,a}} = \frac{Seal\ Diet}{\sum B_{c,a}}$$

$$M_s * \sum PR_a * B_{c,a} = Seal\ Diet$$

And thus

$$M_s = \frac{Seal\ Diet}{\sum PR_a * B_{c,a}} \tag{A.3}$$

In the ADAPT, a first run is conducted assumed that annual percent cod in seal diet during the time series is zero. This provides an estimate of average total cod biomass during 1991–1998 which is used to estimate q (Eq. (5)) and thus P_t using the type II functional response (Eq. (4)). The model is rerun until the 1991–1998 average total cod biomass remains unchanged. In practice, this took one–two iterations. At each time step in the ADAPT, the VPA equation is solved working backwards (Newton–Raphson), assuming a value of M_s and the population abundance at the beginning of the time period (N_a) and the fishing mortality during the time period (F_a) estimated. These are then used in Eq. (A.3) to estimate M_s (Newton–Raphson) and the VPA equation re-estimated. The two equations are iteratively solved until convergence of F_a and M_s .

Appendix B.

Parameter uncertainties estimated at solution (asymptotic variances) of ADAPT model assuming PMAX of 22%, flat top selectivity and 7% cod in grey seal diet during 1991–1998. Note: align numbers in Std. Err. column.

Parameter	Ln estimate	Std. Err.	Rel. Err. (CV)
N2009, age 1	9.7598	0.76506	0.078
N2009, age 2	9.4875	0.57069	0.06
N2009, age 3	10.05222	0.51881	0.052
N2009, age 4	9.55006	0.49697	0.052
N2009, age 5	10.16584	0.47796	0.047
N2009, age 6	9.04055	0.47	0.052
N2009, age 7	8.17589	0.46987	0.057
N2009, age 8	7.2166	0.47641	0.066
N2009, age 9	6.43257	0.51979	0.081
N2009, age 10	6.14315	0.55242	0.09
N2009, age 11	5.63977	0.57466	0.102
N2009, age 12	5.23118	0.59498	0.114
N2009, age 13	3.75843	0.62532	0.166
N2009, age 14	3.92414	0.66715	0.17
N2009, age 15	3.46653	0.70205	0.203
N2008, age 15	2.82662	0.62405	0.221
N2007, age 15	1.99036	0.63563	0.319
N2006, age 15	2.51169	0.62886	0.25
N2005, age 15	2.37648	0.6126	0.258
N2004, age 15	2.04435	0.62392	0.305
N2003, age 15	2.42921	0.62883	0.259
N2002, age 15	3.35025	0.6223	0.186
N2001, age 15	2.99166	0.71175	0.238
N2000, age 15	3.00723	0.78541	0.261
N1999, age 15	3.14296	0.7945	0.253
N1998, age 15	3.49503	0.83234	0.238
N1997, age 15	4.5948	0.88638	0.193
N1996, age 15	4.98822	0.85353	0.171
N1995, age 15	6.19116	0.85302	0.138
N1994, age 15	5.78373	1.11717	0.193
N1993, age 15	5.75481	1.16118	0.202
N1992, age 15	6.54806	0.91169	0.139
N1991, age 15	5.08492	2.38788	0.47
N1990, age 15	6.50885	0.83309	0.128
N1989, age 15	6.87137	0.71907	0.105
N1988, age 15	6.46236	0.77953	0.121
N1987, age 15	6.36675	0.70882	0.111
N1986, age 15	6.18476	0.66776	0.108
N1985, age 15	4.16583	1.99907	0.48
$M_{other, 1986/1988}$	-1.05246	0.29068	0.276
Dev 1989/1991	-1.35260	1.39213	1.029
Dev 1992/1994	1.72169	1.38167	0.803
Dev 1995/1997	0.04053	0.41	10.117
Dev 1998/2000	-0.69702	0.61938	0.889
Dev 2001/2003	0.71223	0.6145	0.863
Dev 2004/2006	-1.87375	1.8375	0.981
Dev 2007/2009	-4.50921	181.32184	40.211

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