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**Estimating the Impact of Grey Seals on
the Eastern Scotian Shelf Cod
Population to 2009**

**Estimation de l'impact du phoque gris
sur les populations de morue des
parties orientale du plateau néo-
écossais jusqu'en 2009**

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ABSTRACT

The cod-seal, predator-prey model of Trzcinski et al. (2006) was used to estimate the total consumption by grey seals on the Eastern Scotia Shelf (ESS, NAFO: 4VsW) and the impact of grey seals on cod recovery up to 2010. New data included the 2010 estimate of Gulf of St. Lawrence and Sable Island pup production and cod catch-at-age data to 2009. Data from satellite tracking was updated. There was little change in the estimate of the proportion of grey seals using the ESS. There was no new data on seal diet using fatty acid signature analysis. New data and analysis of otoliths collected from scat were used as the basis for an alternative diet scenario. As in Trzcinski et al. (2009), a model constraint was used so that cod removals-at-age could not exceed the estimate of cod abundance at age.

On the ESS, cod comprised on average less than 2% of a grey seals diet. The updated model produced lower estimates of natural mortality than Trzcinski et al. (2006). Four scenarios of seal diet were run: 1) 7% cod in seal diet and age distribution of cod eaten estimated from scats, 2) 7% cod in seal diet and age distribution of cod eaten shifted to older cod using RV survey data, 3) 2% cod in seal diet from fatty acids and age distribution of cod eaten estimated from scats, and 4) 2% cod in seal diet from fatty acids and age distribution of cod eaten shifted to older cod using RV survey data. These scenarios were selected to explore the consequences of uncertainty in the proportion of cod in the diet and potential bias caused by regional foraging by seals in areas of small / young cod. These scenarios were selected to explore the consequences of uncertainty in the proportion of cod in the diet and potential bias caused by regional foraging by seals in areas of small / young cod. The updated model showed that in 2009 grey seals imposed a low level of instantaneous mortality under the four scenarios (0.013, 0.021, 0.087, 0.166), which ranges from approximately 2 to 22% of the total mortality (0.75).

RÉSUMÉ

Le modèle prédateur-proie appliqué à la morue et au phoque par Trzcinski et al. (2006) a servi à estimer la consommation totale de morue par le phoque gris dans l'est du plateau néo-écossais (EPN.-É., div. 4VsW de l'OPANO) et l'incidence du phoque gris sur le rétablissement de la morue jusqu'en 2010. Les nouvelles données examinées comprenaient l'estimation de la production de bébés phoques dans le golfe du Saint-Laurent et à l'île de Sable en 2010, ainsi que les données sur les captures de morue selon l'âge jusqu'en 2009. Les données de repérage par satellite ont été mises à jour. Il y avait peu de changement dans l'estimation de la proportion de phoques gris évoluant dans l'est du plateau néo-écossais et pas de nouvelles données sur l'alimentation des phoques obtenues par analyse de la signature des acides gras. Les données nouvelles et l'analyse des otolithes provenant d'excréments de phoque ont été utilisées pour formuler d'autres scénarios de régime alimentaire. Comme dans Trzcinski et al. (2009), une contrainte a été intégrée au modèle afin que les prélèvements selon l'âge parmi la morue n'excèdent pas l'estimation de l'abondance selon l'âge chez cette dernière.

Dans l'est du plateau néo-écossais, la morue représentait en moyenne moins de 2 % de l'alimentation des phoques gris. Le modèle actualisé a produit des estimations de la mortalité naturelle inférieures à celle du modèle de Trzcinski et al. (2006). Quatre scénarios de régime alimentaire des phoques ont été considérés : 1) une proportion de 7 % de morue dans l'alimentation du phoque, avec estimation de la répartition des âges des morues consommées fondée sur l'analyse d'excréments de phoque; 2) une proportion de 7 % de morue dans l'alimentation du phoque, avec répartition des âges des morues consommées provenant cette fois des données du relevé NS et axée sur des morues plus âgées; 3) une proportion de 2 % de morue dans l'alimentation du phoque d'après l'analyse des acides gras, avec estimation de la répartition selon l'âge des morues consommées fondée sur l'analyse d'excréments de phoque et 4) une proportion de 2 % de morue dans l'alimentation du phoque d'après l'analyse des acides gras, avec répartition des âges des morues consommées provenant des données du relevé NS et axée sur des morues plus âgées. On a choisi ces scénarios pour explorer les conséquences de l'incertitude quant à la proportion de morue présente dans l'alimentation et le biais possible causé par la quête alimentaire des phoques dans les zones de la région où évoluent de petites ou jeunes morues. Le modèle actualisé révélait qu'en 2009 la mortalité instantanée imputable aux phoques gris était faible selon les quatre scénarios (0,013, 0,021, 0,087 et 0,166), allant de 2 à 22 % environ de la mortalité totale (0,75).

INTRODUCTION

There has been a long-standing concern among fishermen about the impact of seals on fish stocks. Fishermen often view seals as a competitor that will negatively affect their ability to make a livelihood. There is no doubt that seals eat fish and some of the fish they eat are also sought after by fishermen, but in a complex ecosystem like the North Atlantic we cannot then infer that more seals mean less fish for fishermen or a less productive ecosystem. To assess the impact of predation on a particular species or stock, at a minimum one needs to estimate the amount of the prey species consumed by the predator population and the fraction of the prey population represented by that consumption.

Fishing led to the massive decline of cod stocks throughout the North Atlantic some 15 years ago (Myers et al. 1997). Since then fisheries scientists and the public have been asking “Why have these stocks failed to recover in the absence of fishing?” There have been many hypotheses put forward including: unreported catch, disease, contaminants, starvation, life-history change, impacts of increased seal abundance including predation, parasites and indirect effects, and increased predation by other predators (DFO 2003, 2009b; Dutil et al. 2003). These factors may act in concert, and the data used to discriminate among them is weak. None-the-less, predation by grey seals in the Gulf of St. Lawrence and on the Scotian Shelf has been viewed as the hypothesis with the most support.

We used a predator-prey model which incorporates seal abundance, seasonal distribution, energy requirements, and diets to estimate total consumption of prey by grey seals, as in Trzcinski et al. (2006). This model was developed for the Eastern Scotian Shelf (ESS) and used cod data up to 2003 and seal data up to 2004. Here we updated the ESS model to 2009. We provide estimates of the grey seal population abundance for Sable Island, small inshore breeding colonies along the eastern shore of Nova Scotia, and the southern Gulf of St. Lawrence. We estimate total consumption by grey seals, and their consumption of cod. The consumption of cod was translated into an instantaneous mortality and the impact of grey seals on cod recovery was quantified by comparing seal predation mortality with fishing mortality and natural mortality due to other sources.

METHODS

We used basically the same model and data sources as Trzcinski et al. (2006), but made several changes to the model and updated the model with new data. We quantified the impact of grey 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 seasonal energetic model, 3) estimating seasonal use of the ESS from satellite tracking data, 4) using estimates of the percent cod in the total diet, and the size-specific selectivity of cod consumed, and 5) modeling a grey seal functional response. The model was constructed using AD Model Builder (Fournier 1996). The model was 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 grey seal population trends. We incremented our predator-prey model on a quarterly basis. The methods below are a condensed version of those used by Trzcinski et al. (2006), which focuses on changes made to the model. The description of state variables and parameters, and the full set of equations can be found in Appendices A and B.

The data input to the cod and seal models were revised and updated. With respect to the cod data, time series of survey catch at age, survey weight at age and commercial catch at age were revised and extended up to and including 2009. Sable Island seal pup count data from

2010 was used. The model was not fit to cull data for the Sable Island population and pup counts along the Eastern Shore as pup mortality could not be estimated well when these data were included. Exclusion of the cull data and Eastern Shore pup counts will cause the total population estimates to be biased low, but this bias should be small due to the small size of the Eastern Shore herd (relative to Sable Island) and the relatively small culls on Sable.

Structural changes were also made to the cod and seal models. The age distribution of cod in the first year (1970) was reparameterized. Previously the number of fish of each age was estimated separately. We reduced this distribution to one estimated parameter, the number of one-year-old fish, and calculated the number of fish of older ages assuming age-specific natural (M) and fishing (F) mortalities from the first year as estimated by the model. Also, all selectivity parameters in the cod model were fixed at their maximum likelihood values. These alterations to the cod model improved the performance of the MCMC algorithm (discussed below). As in Trzcinski et al. (2006, 2009), the Sable Island seal population was modeled as a theta-logistic function of total population size, which was assumed to affect both pup and juvenile survival. Following the pattern assumed in Mohn and Bowen (1997), the prior on adult male mortality was assumed to be twice that of adult female mortality.

The model contains a constraint so that cod removals at age by grey seals can not exceed the estimate of cod abundance at age. As in Trzcinski et al. (2006), the natural mortality in 1970 was given a prior of $M=0.2$ with a normal distribution and a $\sigma = 0.2$. Changes in natural mortality were estimated using a 4-parameter logistic function.

The cod and seal models were then integrated into a single estimation process with feedback between the models. Parameter estimation in this joint model involved an iterative phase where the seal and cod models were run sequentially and repeatedly until model quantities had converged. We fixed the number of iterations to four, which seemed to be sufficient for convergence near the maximum likelihood values. Thus, within each iteration of the parameter estimation algorithm, the cod and seal models are iterated four times.

We also conducted a preliminary MCMC run with the joint model. The results of the MCMC were broadly similar to the maximum likelihood results with respect to some model quantities (e.g., seal population size), but not others (e.g., cod natural mortality, consumption of cod by seals). There was also poor convergence/sampling for some model quantities. Nevertheless, overall the results of the MCMC run were promising for being able to better characterize the uncertainty in estimates from this joint model.

Four scenarios of seal diet were run: 1) 7% cod in seal diet and age distribution of cod eaten estimated from scats, 2) 7% cod in seal diet and age distribution of cod eaten shifted to older cod using RV survey data, 3) 2% cod in seal diet from fatty acids and age distribution of cod eaten estimated from scats, and 4) 2% cod in seal diet from fatty acids and age distribution of cod eaten shifted to older cod using RV survey data. These scenarios were selected to explore the consequences of uncertainty in the proportion of cod in the diet and potential bias caused by regional foraging by seals in areas of small / young cod. These scenarios were selected to explore the consequences of uncertainty in the proportion of cod in the diet and potential bias caused by regional foraging by seals in areas of small / young cod.

The functional response of grey seals to changes in cod density is unknown. Therefore we analyzed our model under 2 assumptions about feeding rates. Our data on the proportion of cod in the diet, from the Quantitative Fatty Acid Signature Analysis (QFASA) model, exhibited interannual variability but little evidence of an annual trend. Thus in one case, we assumed 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., Assenbourg et al. 2006).

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:

$$nc_a = \frac{\bar{E}}{StomW} p_a,$$

where \bar{E} is the mean biomass of cod eaten from the constant ration model for 1993, $StomW$ is mean weight of cod consumed from 1970 to 2007, and p_a the proportion of cod consumed at age. The interaction between cod and seals was then calculated as:

$$q_a = \frac{nc_a}{C_a \bar{N}},$$

where (nc_a) is the number of cod consumed at age in 1993, C_a is the mean number of cod at age, and \bar{N} the mean number of seals on the ESS in 1993. It is often observed that predator consumption rates increase with prey density up to a maximum level. We did not have enough data over a wide enough range of cod biomass to directly estimate the parameters of a hyperbolic functional response. We pieced together a hyperbolic functional response by using the maximum proportion of cod in the diet (f_{1+}) calculated from scat samples from 1991-1997 (Bowen and Harrison 2007) to calculate the asymptotic attack rate ($q_{a,max}$). This approach is reasonable because grey seal scats represent a 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 $f_{1+} = 0.22$, recalculating the biomass of cod eaten and the number of cod eaten (as in Trzcinski et al. 2006 equations 10 and 12), and then recalculating $q_{a,max}$ as:

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

We assumed that the q_a 's derived from QFASA provide a reasonable estimate of attack rates at low cod abundance because cod was at extremely low abundance from 1993-2000. If we then assume a hyperbolic functional response, the number of cod eaten is given by:

$$NE_{t,a} = \frac{q_a C_{t,a}}{1 + \frac{q_a C_{t,a}}{q_{a,max}}} N_t \frac{StomW_t}{StomW}.$$

The model incorporates parameter uncertainty in 2 ways. The means and variances of several parameters in the seal population dynamics model were estimated directly from the pup count data, by minimizing an objective function that is the negative log likelihood of observed and predicted pup numbers. However, the majority of parameters were taken from other studies (Appendix 1 in Trzcinski et al. 2006). 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 act as penalty functions (e.g. Breen et al. 2003). In both cases, variances 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 grey 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 1 in Trzcinski et al. 2006).

The new data included the 2007 and 2010 estimate of Gulf, Sable, and eastern shore of Nova Scotia pup production (Bowen et al. 2007, Thomas et al. 2007, Hammill et al. 2007, DFO unpublished data, Bowen et al. unpublished) and catch-at-age data to 2009. Data from satellite tracking was updated (satellite tracking results: Breed 2008, Breed et al. 2009). These data were used to calculate the proportion of the Sable Island and Gulf of St. Lawrence grey seal populations foraging on the ESS. The proportion of cod-at-age consumed by grey seals was recalculated in Trzcinski et al. (2009), which resulted in more 1 year olds being eaten. Fatty acid estimates of grey seal diets, collected in 2003 and 2004 were incorporated in Trzcinski et al. (2009) and here, and no new estimates are available. As done previously, the size composition of cod in a seal's diet was reconstructed from otoliths collected from seal scats (Bowen and Harrison 2007). Cod lengths were converted to a proportion of cod at age using the ageing data from the annual DFO groundfish research survey. To explore the consequences of grey seal foraging on older cod we used the July research vessel survey data on numbers at age, to generate a size composition of cod in the seal diet that was shifted to older fish. The results of both the constant ration and functional response models are presented.

RESULTS

The population size of grey seals used to initialize this version of the model in 1962 was estimated to be 422 ± 35.8 SE. This value is higher than in Trzcinski et al. (2006; 392 ± 25 SE), but lower than Trzcinski et al. (2009; 546 ± 28.9 SE). Even with new tracking data there was little change in the estimate of the proportion of grey seals on the ESS (Table 1 compared to Table 2 in Trzcinski et al. 2006), and one can see that most of the Sable Island population foraged on the ESS. The proportions of cod consumed at age were taken from Figure 1 in Trzcinski et al. (2009). The cut-off points for the cod length at age categories resulted in more 1 year olds being eaten than in Trzcinski et al. (2006). The length-at-age categories used here were derived from the length at age data from the Groundfish Research Vessel Survey from 1970 to 2007 (Branton and Black 2004). The inclusion of the 2003 and 2004 diets based on fatty acids confirms that adult grey seals consume a low and variable proportion of cod, and there is some evidence for a decline in the proportion of cod in the diet of young grey seals based on these data (Figure 1). An independent estimate of grey seal diet composition comes from otolith recovered in scats from Sable Island during the period 1991 to 2010 (Bowen et al. WP# 4). These data indicate a higher mean percentage of cod (7%) with no evidence of significant seasonal variation or inter-annual trend in the percentage of cod in the diet.

Pup production has continued to increase, but the rate of increase is slowing indicating that density dependence is presumably influencing demographic rates (Bowen et al. 2007, Bowen et al. 2010, Figure 2). The Sable Island population is estimated to be 261,290 ($\pm 24,751$ SE). Given a theta of 2.4 and the assumption that density dependence affects pup and juvenile survival only, carrying capacity was estimated at 295,280 ($\pm 30,330$ SE). The Gulf population is highly variable and dependant on ice conditions. Overall, the population has been increasing and is estimated to be 54,730 ($\pm 4,739$ SE, Figure 3). When movement is accounted for, there are anywhere from 164,000 to 234,000 grey seals from these two populations feeding on the ESS (Figure 4). In relative terms, this is anywhere from 62 to 90% of the Sable Island population.

On the ESS, a catch-at-age stock assessment model shows that cod have decreased at an average rate of 17% per year from 1984 to 2007, a 96% decline in spawning stock biomass (Figure 6a). However, catch rates of cod on the ESS have been relatively high in three of the last four years in the groundfish RV survey. Age data indicate that a relatively high recruitment event occurred in 2004. Grey seals consumed an estimated 288,725 t of prey on the ESS. The constant ration model assumes that 2 or 7% of a grey seals diet is cod and that this consumption rate is constant regardless of prey availability. Consequently, the estimate of the number of cod eaten is proportional to seal abundance ranging from 4,000 to 100,000 (Figure 7). The functional response model allows the percent cod in the diet to vary with prey availability. Depending on the assumed seal diet, cod comprised between 5 and 40% of a grey seals diet when cod were abundant in the 1980s. Currently they comprise between 0.3 and 6.8% of the diet and grey seals are estimated to have eaten between 1,350 ($\pm 7,888$ SE) and 13,723 ($\pm 7,469$ SE) tons of cod in 2009. This new model run using the functional response produced lower estimates of predation mortality than Trzcinski et al. (2006) and similar to Trzcinski et al. (2009). The updated model showed that in 2009 grey seals imposed a low level of instantaneous mortality (scenarios: 0.013, 0.021, 0.087, 0.166), which ranges from approximately 2 to 22% of the total mortality (0.75) (Figure 8). Our current estimate of mortality due to seal predation is within 2SE of the mean estimate in Trzcinski et al. (2006).

DISCUSSION

Using an energetically based predator-prey model, we have shown that grey seal predation forms a small component of the total mortality of cod on the Eastern Scotian Shelf. Assumptions of our analysis include the dynamic-pool assumption of both the cod and seal models, which assumes no spatial structure within the ESS, that *all* grey seals eat a small proportion of cod based on fatty acid analysis, and that large cod are rarely eaten relative to their availability (Bowen and Harrison 2007). We know that the first 2 of these assumptions are not true. The fatty acid and scat of grey seals diets indicates that most seals eat little or no cod but a relatively few seals eat a high proportion of cod (Beck et al. 2007, W. D. Bowen unpublished). As expected seal predation mortality on cod is greater if the percentage of cod in the diet is higher and if older fish are eaten. However, in each case a relatively small fraction of total mortality is accounted for by seal predation.

Spatially-explicit models of predator-prey or parasitoid-host dynamics have shown that the spatial aggregation of the predator can destabilize the system by causing local extinctions if the predator is highly mobile relative to their prey and can quickly aggregate in areas of high prey density (Murdoch et al. 2003, p. 366). Some scientists and fishermen have argued that this is precisely the case with seals aggregating on spawning cod, thereby increasing their impact and preventing recovery. This is a reasonable hypothesis, but there currently is little data which can be used to test it other than noting that otoliths from large cod are infrequently found in grey

seal scats from Sable Island or along the coast of Nova Scotian (Bowen et al. 1993, Trzcinski et al. 2006), although they are more prevalent in the Southern Gulf of St. Lawrence (e.g., Hammill et al. 2007). Others have criticized the diet data going into the model, claiming that grey seal diet data collected in Scotland, principally from otoliths collected from scats, show that cod is a larger part of a grey seal's diet. While we acknowledge that this very well could be true for that region, it does not follow that data collected on the ESS are not representative of what is being eaten on the Scotian Shelf. Undoubtedly, there is large uncertainty in the estimates of diet in both regions, and Trzcinski et al. (2006) incorporated this uncertainty for the ESS and partitioned it into several components. While the uncertainty in the diet remains the largest component, it seems unlikely that we will be able to reduce this uncertainty with more data in the near future. Bias in the diet data is more difficult to evaluate, but foraging studies currently being conducted on grey seals using animal-borne cameras and 'business card' acoustic tags may help resolve this debate.

Our estimates of cod biomass should not be thought of as the accepted assessment for the ESS. Our estimates of cod biomass differ from the assessments in other areas (e.g. DFO 2009a) because we allow the model to estimate a time varying natural mortality. Under this scenario, the model converges on a high natural mortality due to sources other than that explicitly modeled in the seal-cod predator-prey model. Higher natural mortality results in a large population biomass and a lower relative impact of grey seals. We argue that this approach is necessary in our context because it allows for the estimate of seal consumption, which is based on the number of seals and a coupling coefficient to be placed in the context of unknown natural mortality. Our assessment models converge with the estimates from accepted stock assessments when the same patterns in natural mortality are used.

Our new estimate of grey seal predation mortality on ESS cod are less than reported in Trzcinski et al. (2006). We now estimate 2.1 times more cod in 1993, the year the coupling coefficient is estimated (Trzcinski et al. (2006): 18,117 t, current model: 39,452 t), resulting in a much weaker interaction coefficient (q_a , equation 13 in Appendix B, Trzcinski et al. 2006). This change between studies emphasizes the importance of the interaction parameter on the estimate of mortality due to seal predation.

There are several avenues for improving our estimate of seal impacts on cod. There is growing uncertainty in the dynamics of the Sable Island grey seal population as density dependence continues to manifest itself. We have chosen to place all density dependence in pup and juvenile mortality, but fecundity may be decreasing as well. Whether density dependence is manifested as pup and juvenile mortality or as a reduced fecundity can have a 2x effect on our current estimate of population size (Thomas and Harwood 2009). Consequently, it is important to continue to monitor the population. We do not have the data to estimate changes in fecundity, but we are in the process of estimating changes in adult survival using mark recapture data. Incorporating these data into our model estimating seal population dynamics will be an important next step.

The model can also be improved by better estimating the grey seal functional response. The asymptotic consumption at low prey size is probably underestimated, as our value comes from a period of low cod abundance but is greater than zero nonetheless. The properties of the functional response at low cod abundance may be particularly important as there could be a switching away from cod consumption (Type 3 functional response), but we currently have little data to evaluate this possibility. In this study, grey seals feeding rates only responded to cod abundance and not to the availability of other species. A multi-species functional response is likely to be more realistic and may produce different results; it has not yet been examined in our model and could be an important avenue for future research. We parametrically estimated

changes in natural mortality. A more flexible method of estimation, such as a random walk may provide additional insights into the impact of grey seal on cod. The current model is fundamentally a 2-species predator-prey model. Understanding the greater role of grey seals in the ecosystem can be gained by placing a simplified version of this model in multi-species framework. Finally, the model is fundamentally a large, dynamic pool model where predators and prey are assumed to mix and interact freely. A new generation of models which incorporates spatial effects in distribution and foraging could aid us in our understanding of the broader implications of grey seal foraging on prey dynamics and ecosystem function.

In summary, the overall conclusion about the relative impact of grey seals on the recovery of ESS cod from this work differs little from that of Trzcinski et al. (2006). Grey seals have and presumably continue to have a small impact on ESS cod relative to the total mortality experienced by this stock.

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Table 1. The percentage of the Sable and Gulf and grey seal populations inhabiting the Eastern Scotian Shelf (ESS) by quarter. The Sable estimates are separated by 3 categories: young of the year (YOY), and adult males and females (n = 24, 59, 69 tracts, respectively from 152 seals). The Gulf population estimates are for combined ages (n = 73 individuals). Estimates were derived using a state-space movement model similar to Breed et al. (2009)..

Population	Category	Quarter (%)			
		1 st	2 nd	3 rd	4 th
Sable	YOY	90	91	93	99
	Male	64	85	79	87
	Female	91	83	69	90
Gulf	All	37	27	1	7

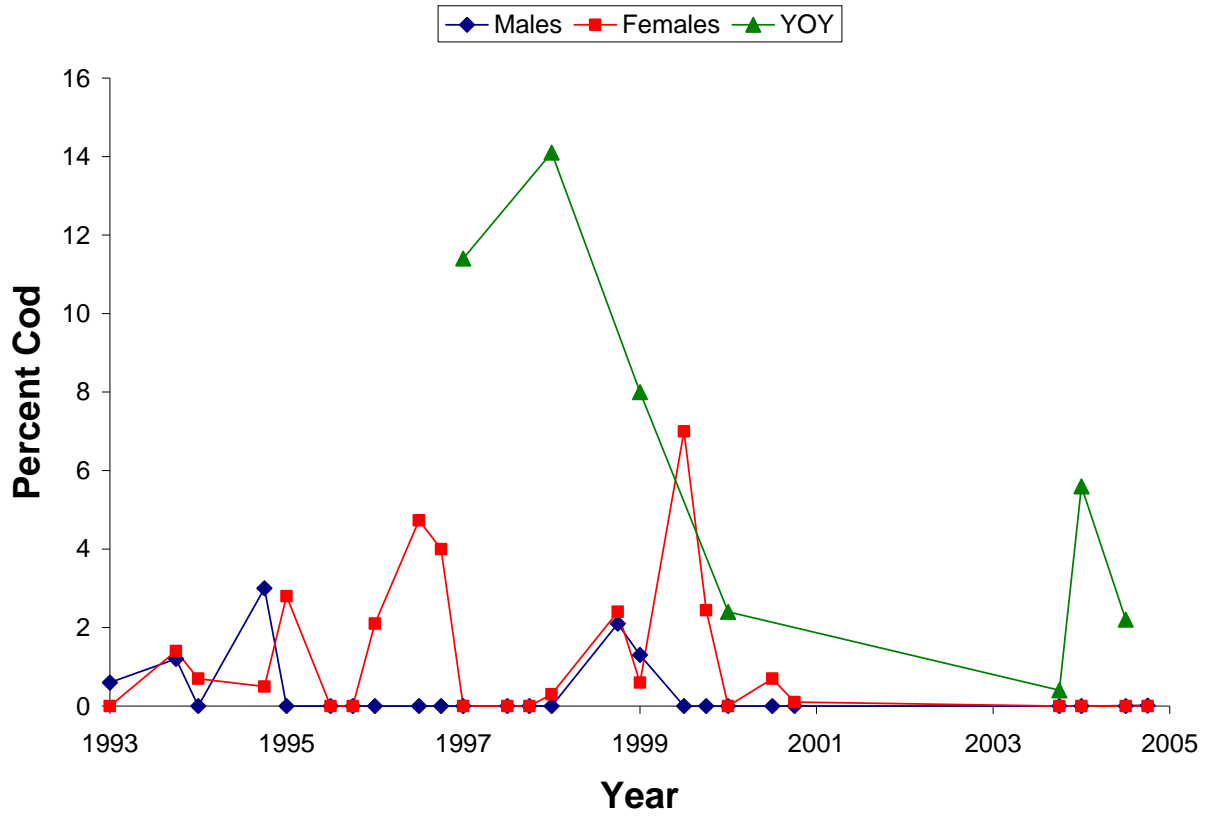


Figure 1. The percent cod in male, female, and young of the year (YOY) grey seal diet estimated from quantitative fatty acid signature analysis (QFASA). Values from 1993 to 2000 were used in Trzcinski et al. (2006). The values for 2003 and 2004 have been incorporated into the overall estimate used in this analysis.

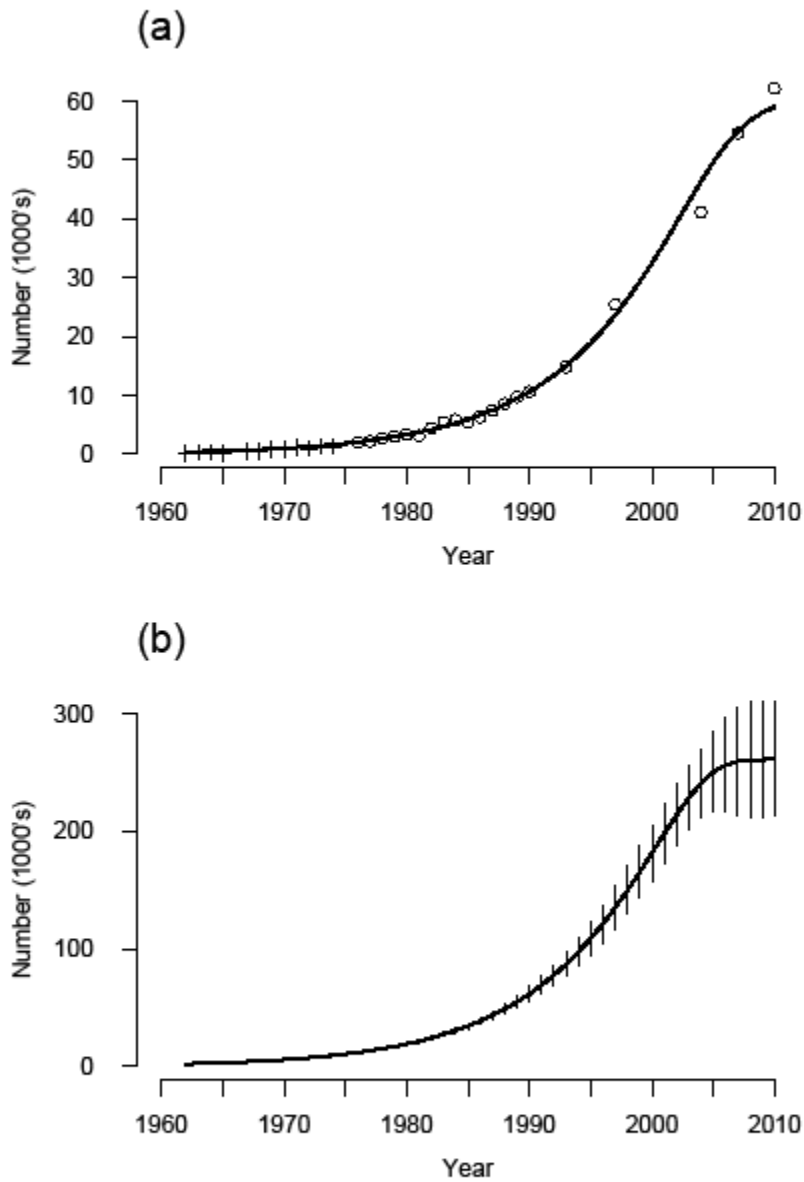


Figure 2. Census counts and model fit (solid line) to the pup production of the Sable Island grey seal population (a). Model estimates of total population size (b). Horizontal lines indicate the 95% C.I.

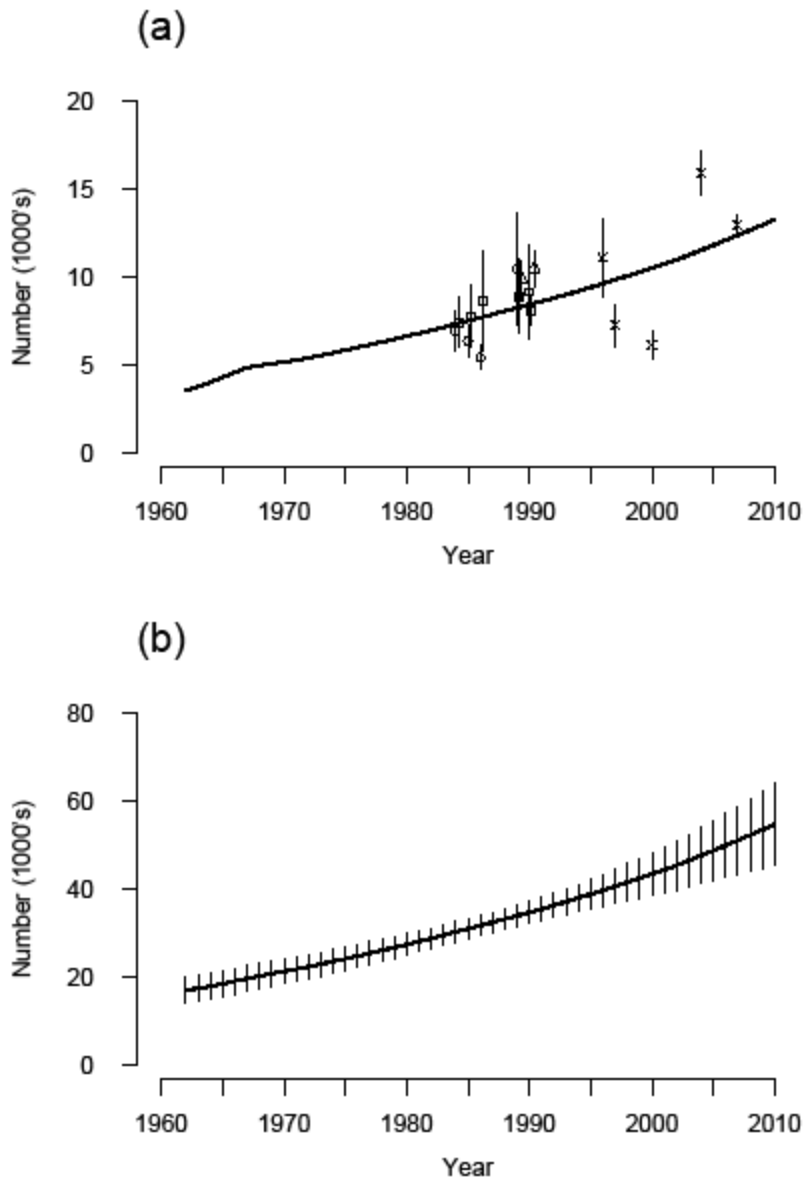


Figure 3. Census counts and model fit (solid line) to the pup production of the Gulf of St. Lawrence grey seal population (a). Model estimates of total population size (b). Horizontal lines indicate the 95% C.I.

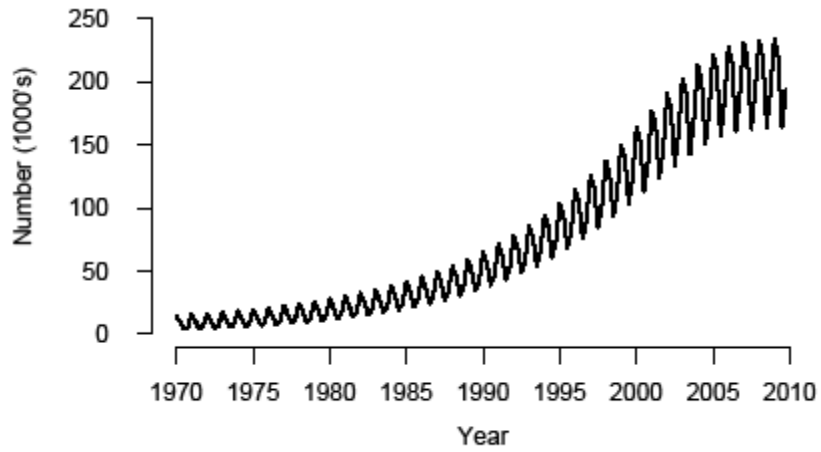


Figure 4. Estimated total number of grey seals on the Eastern Scotian Shelf accounting for population trends and immigration and emigration.

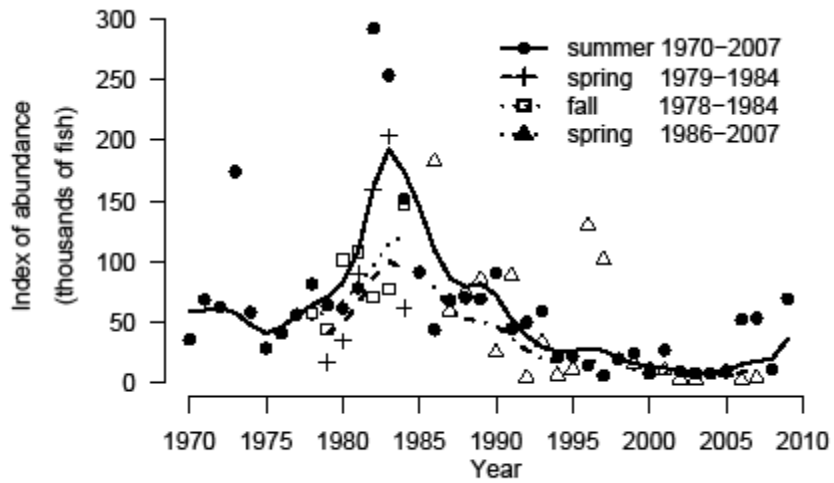


Figure 5. Observations (points) and model fit (lines) to the Scotian Shelf RV surveys.

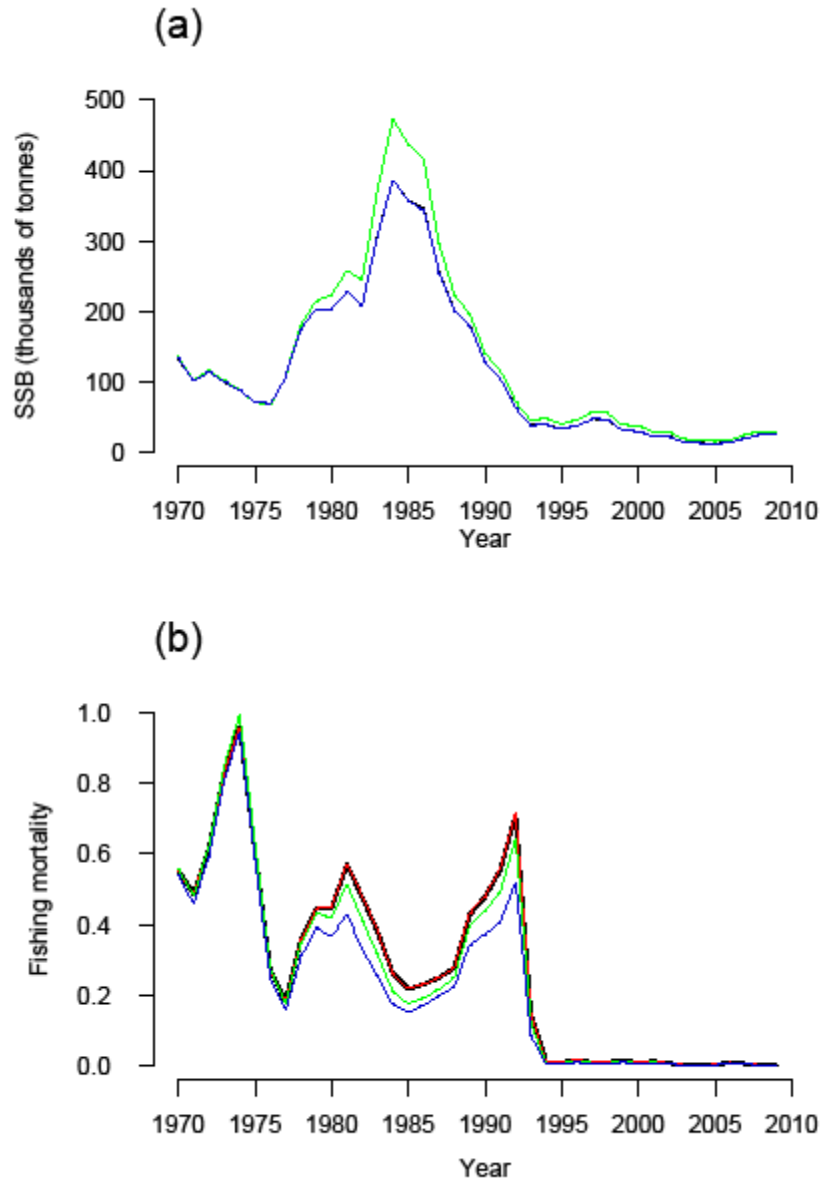


Figure 6. The estimated trends in the Eastern Scotian Shelf cod spawning stock biomass (SSB) and fishing mortality using four scenarios of seal predation on cod.

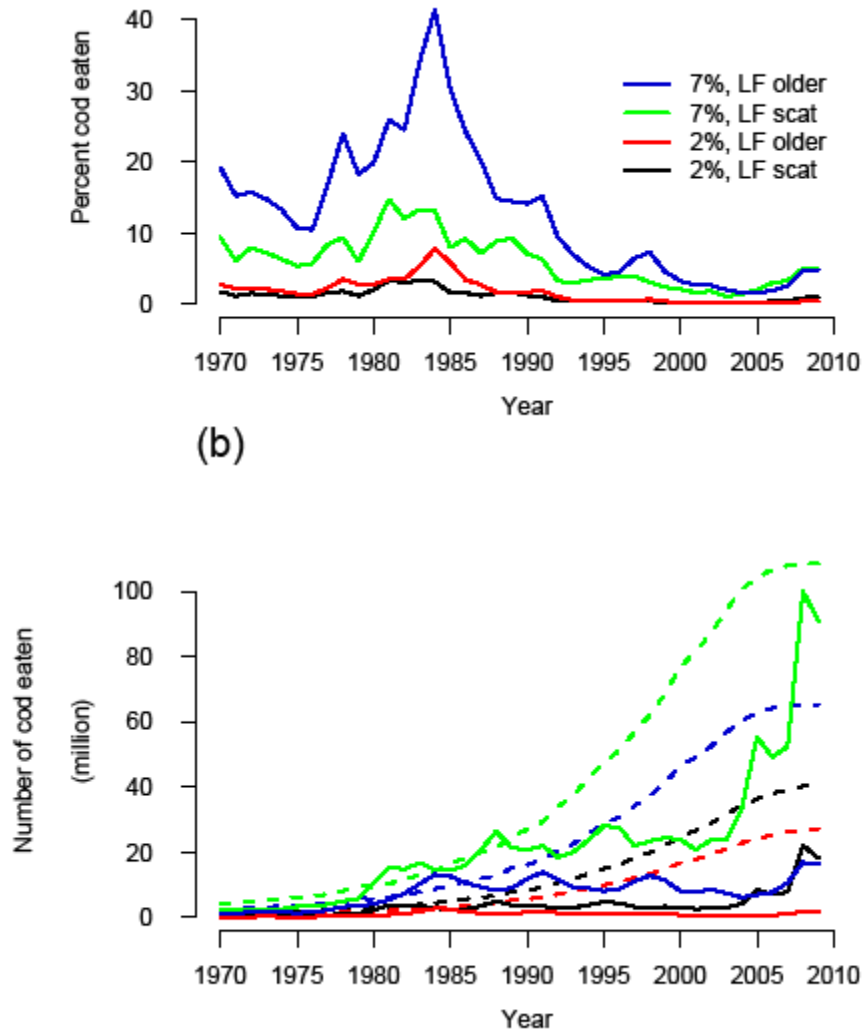


Figure 7. Using four scenarios of seal predation on cod, results of the constant ration (dashed line) and the functional response model (solid line) for the percent cod in grey seal diet (a) and the numbers of cod consumed by grey seals (b) on the Eastern Scotian Shelf using four scenarios of seal predation on cod.

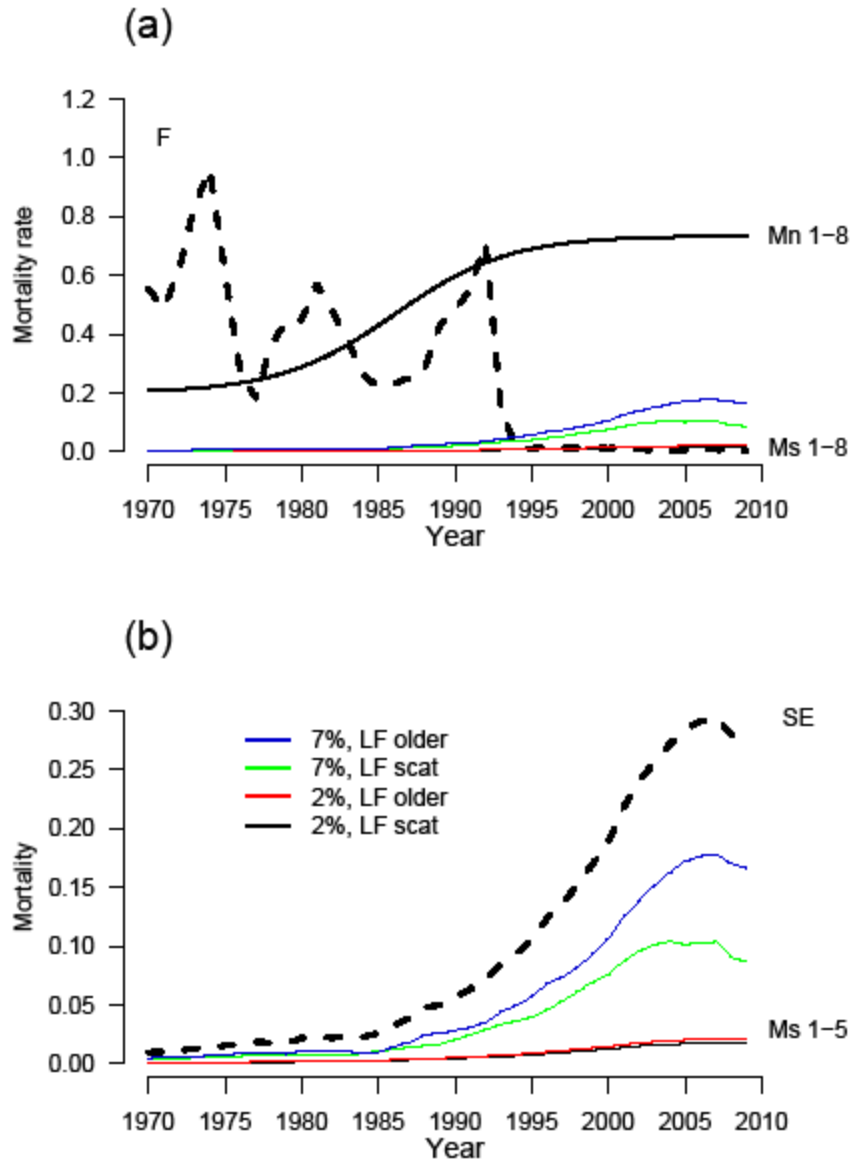


Figure 8. Using four scenarios of seal predation on cod, the instantaneous fishing mortality for fully selected fish (F, dashed line), estimated increased in natural mortality (Mn) for ages 1 to 5, and estimated trend in seal predation mortality (Ms) on ages 1 to 5 from the functional response model for cod on the Eastern Scotian Shelf, (a). The estimated instantaneous mortality rate caused by grey seal predation, (b). The dashed line in (b) is + 1SE estimated from the Hessian approximation of the variance-covariance matrix.

Appendix A. List of state variables and parameters used in the model.

Description	Symbol	
Number of pups	$P_{t+1,s}$	
Number of seals	$N_{t,a,f}$	
Number of juvenile seals	$J_{t+1,1,s}$	
Birth rate at age	b_a	
Carrying capacity	K	
Degree of density dependence	θ	
Natural mortality of pups, juveniles and adults	$-M^{\text{Pup}}$, $-M^{\text{Juv}}$, $-M^{\text{Adult}}$	
Gross energy intake	$GEI_{d,a,s}$	
Body mass	$BM_{d,a,s}$	
Total body energy	$TBE_{d,a,s}$	
Metabolizable energy	ME	
Annual growth rate	$GR_{a,s}$	
Day of the year	d	
Daily rate of change in body mass	$g_{s,i}$	
Biomass needed to maintain seal maintenance and growth	$SG_{q,a,s}$	
Average energy of prey	AE_q	
Proportion remaining on the ESS	$m_{q,a,s}$	
Biomass of cod eaten	E_q	
Fraction of cod in the diet	$f_{q,a,s}$	

Appendix A – Continued -

Number of cod eaten	$NE_{t,a}$	
Mean weight of cod consumed	$StomW_t$	
Proportion of cod consumed at age	p_a	
Number of cod consumed at age	nc_a	
Interaction coefficient	q_a	
Mean number of cod at age	C_a	
Asymptotic attack rate	$q_{a,max}$	
<i>Subscripts</i>		
<i>t</i>	Year	
<i>d</i>	Day	
<i>q</i>	Quarter	
<i>i</i>	Season	
<i>a</i>	Age	
<i>s</i>	Sex	

Appendix B. Equations for the seal / cod predator prey model.

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

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

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

$$A_{t+1,a+1,s} = \left\{ \begin{array}{l} J_{t,a,s} e^{-M^{\text{Juv}}} \\ A_{t,a,s} e^{-M^{\text{Adult}}} \end{array} \right\} \quad (4)$$

$$N_t = \sum_{a,s} P_{t,s} + \sum_{a,s} J_{t,a,s} + \sum_{a,s} A_{t,a,s} \quad (5)$$

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

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

$$SG_{q,a,s} = \frac{\sum GEI_{d,a,s}}{AE_q} (0.000001) \quad (8)$$

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

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

$$NE_{t,a} = \sum_q \frac{E_q}{StomW_t} p_a \quad (11)$$

$$nc_a = \frac{\bar{E}}{StomW} p_a \quad (12)$$

$$q_a = \frac{nc_a}{C_a N} \quad (13)$$

Appendix B – Continued -

$$q_{a,\max} = \frac{nc_a}{N}. \quad (14)$$

$$NE_{t,a} = \frac{q_a C_{t,a}}{1 + \frac{q_a C_{t,a}}{q_{a,\max}}} N_t \frac{StomW_t}{StomW} \quad (15)$$