Fisheries and Oceans Canada / Pêches et Océans Canada
Science / Sciences

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Canadian Science Advisory Secretariat | **Secrétariat canadien de consultation scientifique**

Research Document 2009/052 | **Document de recherche 2009/052**

Estimating the Impact of Grey Seals on the Eastern Scotian Shelf and Western Scotian Shelf Cod Populations

Estimation de l'impact du phoque gris sur les populations de morue des parties orientale et occidentale du plateau néo-écossais

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ISSN 1499-3848 (Printed / Imprimé)
ISSN 1919-5044 (Online / En ligne)

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FOREWORD

This document was not formally peer-reviewed under the Department of Fisheries Oceans (DFO) Science Advisory Process coordinated by the Canadian Science Advisory Secretariat (CSAS). However, it is being documented in the CSAS Research Document series as it presents some key scientific information related to the advisory process.

AVANT-PROPOS

Le présent document n’a pas été revu selon le processus consultatif scientifique du ministère des Pêches et des Océans (MPO), coordonné par le Secrétariat canadien de consultation scientifique (SCCS). Cependant, il est intégré à la collection de documents de recherche du SCCS car il présente certains renseignements scientifiques clés, liés au processus consultatif.

Correct citation for this publication:
La présente publication doit être citée comme suit :

Trzcinski, M.K., R. Mohn, and W.D. Bowen. 2009. Estimating the impact of grey seals on the Eastern Scotian Shelf and Western Scotian Shelf cod populations. DFO Can. Sci. Advis. Sec. Res. Doc. 2009/052. viii + 19 p.

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 Western Scotian Shelf (WSS, NAFO: 4X) and the impact of grey seals on cod recovery up to 2007. New data included the 2007 estimate of Gulf of St. Lawrence and Sable Island pup production and cod catch-at-age data to 2007. Data on hunting removals on Sable Island in the 1960s were incorporated, which put a lower bound on the early population size and increased our estimate of seal abundance for that period. Data from satellite tracking was updated and we provide the first estimate of the number of Sable Island grey seals foraging on the WSS. There was little change in the estimate of the proportion of grey seals using the ESS. The proportion of cod-at-age consumed by grey seals was recalculated, which resulted in more 1 year olds being eaten. Fatty acid estimates of grey seal diets, collected in 2003 and 2004, were also incorporated in the model. A model constraint was added so that cod removals-at-age could not exceed the estimate of cod abundance at age.

In the ESS, cod comprised on average less than 2% of a grey seals diet. The updated model produced significantly lower estimates of natural mortality than Trzcinski et al. (2006). The updated model showed that in 2007 grey seals imposed a low level of instantaneous mortality (0.08), which is approximately 11% of the mortality due to all sources except fishing (0.74) (Figure 8).

On the WSS, our catch-at-age stock assessment model showed that cod have decreased 50% since 1988. As there is no data on the diet of grey seals on the WSS, we assumed that grey seals feeding on the WSS had a similar diet as those on the ESS; i.e., that cod comprises approximately 2% of the diet. Since cod grow faster on the WSS, the proportion of age-1 cod in the diet was estimated to be larger. The proportion of the Sable Island and Gulf of St. Lawrence herd, which foraged on the WSS, was estimated by quarter using satellite tagging data. A higher proportion of males foraged on the WSS than females. The number of seals foraging on the WSS varied by season and was estimated to average 13,322 (± 2,235 SE) in 2007. Our consumption model estimated that grey seals consumed 21,954 t (± 7,897 SE) of prey. Mortality of cod caused by grey seals increased with the increase in the seal population and averaged 0.0012 which is estimated to be approximately 0.2 % of total natural mortality. Fishing (bycatch) mortality of cod (F=0.16) and natural mortality due to sources other than seal predation (Mn – Mseals ~ 0.66) are high and are causing the stock to decline.

RÉSUMÉ

Le modèle prédateur-proie, morue-phoque, de Trzcinski et coll. (2006), a servi à estimer la consommation totale des phoques gris dans la partie orientale (PNE-Est, OPANO : 4VsW) et dans la partie occidentale (PNE-Ouest, OPANO : 4X) du plateau néo-écossais ainsi que l'impact des phoques gris sur le rétablissement de la population de morue jusqu'en 2007. Les nouvelles données comprenaient l'estimation de 2007 de la production des chiots dans la région du Golfe Saint-Laurent et de l'île de Sable, ainsi que les données de prises selon l'âge des morues jusqu'en 2007. On a intégré à l'étude les données sur des captures de phoques par la chasse sur l'île de Sable dans les années 1960, ce qui a permis de déterminer une limite inférieure de la taille de la population à cette époque et d'augmenter les estimations visant l'abondance des phoques pour cette période. On a mis à jour les données des relevés par satellite et on a fourni la première estimation du nombre d'aires de quête de nourriture des phoques gris sur l'île de Sable, dans la division Ouest du PNE. On observe peu de changement dans l'estimation de la proportion de phoques gris fréquentant la partie Est du PNE. La proportion des prises de morues selon l'âge consommées par les phoques gris a fait l'objet d'un nouveau calcul, ce qui a donné pour résultat davantage de proies d'un an consommées. Les données sur les estimations des acides gras dans le régime alimentaire des phoques gris, recueillies en 2003 et en 2004, ont également été intégrées au modèle. Une contrainte a été appliquée au modèle afin que les prises de morues selon l'âge ne puissent pas surpasser l'estimation de l'abondance des morues selon l'âge.

Dans la partie Est du PNE, la morue représentait en moyenne moins de 2 p. 100 du régime alimentaire du phoque gris. Le modèle mis à jour a produit des estimations nettement moins élevées du taux de mortalité naturelle comparativement à celui de Trzcinski et coll. (2006). Le modèle mis à jour indiquait qu'en 2007, les phoques gris ont imposé un niveau très bas de mortalité instantanée (0,08), qui représente environ 11 p. 100 du taux de mortalité par toutes les causes sauf par la pêche (0,74) (Figure 8).

Dans la partie Ouest du PNE, le modèle d'évaluation des prises selon l'âge indiquait que le stock de morue avait diminué de moitié depuis 1988. Puisqu'il n'existe pas de données sur le régime alimentaire des phoques gris dans la partie Ouest du PNE, il est présumé que les phoques gris s'alimentant dans cette zone avaient un régime alimentaire similaire à celui des phoques de la partie Est du PNE, c'est-à-dire que la morue représentait environ 2 p. 100 de ce régime. Puisque la morue croît plus rapidement dans la partie Ouest du PNE, on estime que la proportion de morue d'un an dans le régime alimentaire était plus importante. La proportion du troupeau de phoques de l'île de Sable et du Golfe Saint-Laurent, qui s'alimentaient dans la partie Ouest du PNE, a été estimée par trimestre au moyen de données d'étiquetage par satellite. Une proportion plus élevée de mâles que de femelles étaient en quête de nourriture dans la partie Ouest du PNE. Le nombre de phoques en quête de nourriture dans cette partie Ouest du PNE variait en fonction de la saison et a été estimé en moyenne à 13 322 (erreur-type de ± 2 235) en 2007. Le modèle de consommation a estimé que les phoques gris ont consommé 21 954 tonnes (erreur-type de ± 7 897) de proies. La mortalité chez la morue causée par les phoques gris a augmenté avec l'augmentation de la population de phoque et s'établissait en moyenne à 0,0012, ce qui représentait environ 0,2 p. 100 du taux total de mortalité naturelle. La mortalité par pêche chez la morue (P=0,16) et la mortalité naturelle causée par d'autres sources que la prédation des phoques (Mn – Mphoques ~ 0,66) sont élevées et provoquent un déclin au sein de la population.

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 2007, and also applied the model for the first time to the Western Scotian Shelf (WSS; including the Bay of Fundy). Since both cod and seal abundance differ in the ESS and WSS, comparing the 2 regions should help our understanding of the effect of seal predation on the recovery of cod. 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. On both the ESS and WSS, 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 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 and WSS 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 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., Assenburg 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

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

where $\overline{E}$ 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

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

where (nc_a) is the number of cod consumed at age in 1993, C_a is the mean number of cod at age, and $\overline{N}$ 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

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

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

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

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 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) and catch-at-age data to 2007. Data on hunting removals on Sable Island in the 1960s (Thomas et al. 2007) were incorporated, which put a lower bound on the early population size and increased our estimate of seal abundance for that period. Data from satellite tracking was updated, and we provide the first estimate of the number of Sable Island grey seals foraging on the WSS (tracking results: Breed et al. in press, Breed 2008). These data were used to calculate the proportion of the Sable Island and Gulf of St. Lawrence grey seal populations foraging on the ESS and WSS. The proportion of cod-at-age consumed by grey seals was recalculated, which resulted in more 1 year olds being eaten. Fatty acid estimates of grey seal diets, collected in 2003 and 2004 (n=240 seals), were also incorporated in the model. 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. Since cod grow faster on the WSS, we calculated the proportions of cod at age in the diet separately for the ESS and WSS. As there is no data on the diets of grey seals in the WSS, we assumed that grey seals had a similar diet on the WSS as those on the ESS; that is cod comprises approximately 2% of the diet. Although this assumption should be questioned given the differences in the fish communities between these 2 parts of the Scotian Shelf and the fact that cod are more abundant on the Western Scotian Shelf, we believe it best to use the data from a neighbouring ecosystem.

The only change to the structure of the model was the addition of a constraint so that cod removals at age by grey seals could 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. As in Trzcinski et al. (2006), 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 546 ± 28.9 SE. This value is higher than in Trzcinski et al. (2006) and is primarily due to the incorporation of hunting removals from Sable Island in the 1960s, which put a lower bound on the population size. 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. Females and young of the year spent little or no time on the WSS, but a larger proportion males foraged there (Table 1b). In this model, 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) (Figure 1). 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 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 (Figure 2).

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, Figure 3). The Sable Island population is estimated to be 241,270 (± 3,075 SE). The Gulf population is highly variable and dependant on ice conditions. Overall, the population has been increasing and is estimated to be 51,032 (±3,940 SE, Figure 4). Grey seals move long distances to forage (Breed et al. in press), and there is wide seasonal variation in seal abundance on the ESS and WSS (Figure 5).

On the ESS, a catch-at-age stock assessment model shows that cod have decreased at an average rate of 17% per year since 1984, a 96% decline in spawning stock biomass (Figure 6a). Grey seals consumed an estimated 275,380 t of prey on the ESS. The constant ration model assumes that 2% 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 (38,164 ± 11,714 SE, Figure 7). The functional response model allows the percent cod in the diet to vary with prey availability. When cod were abundant in the 1980s, cod comprised approximately 5% of a grey seals diet. Currently they comprise less than 2% of the diet and grey seals are estimated to have eaten 3,216 (± 7,722 SE) cod in 2007 (Figure 7). This new model run using the functional response produced lower estimates of predation mortality than Trzcinski et al. (2006). The updated model showed that in 2007 grey seals imposed a low level of instantaneous mortality (0.08), which is approximately 11% of the mortality due to all sources except fishing (0.74) (Figure 8). Our current estimate of mortality due to seal predation is within 2SE of the mean estimate in Trzcinski et al. (2006).

On the WSS, a catch-at-age stock assessment model showed that the cod population has been slowly declining since 1988, and that the spawning stock biomass is now 50% of what it was in 1988 (Figure 6b). Grey seals consumed an estimated 21,954 t (± 7,897 SE) of prey on the WSS. Since cod grow faster on the WSS, the proportion of age-1 cod in the diet was estimated to be larger (Figure 9). The number of seals foraging on the WSS varied by season and was estimated to average 13,322 (± 2,235 SE) in 2007 (Figure 5). The seal-cod functional response model estimates that the proportion of cod in the diet averages 0.2% in 2007 and grey seals are estimated to have eaten 55 (± 385 SE) cod in 2007 (Figure 10). Mortality caused by grey seals has increased with the seal population and averages 0.0012 which is estimated to be approximately 0.2 % of total mortality. Fishing mortality is high (0.16) and along with high natural mortality due to other sources (approximately 0.66) is causing the stock to decline (Figure 11).

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 and, presumably, Western Scotian shelves. Assumptions of our analysis include the dynamic-pool assumption of both the cod and seal models, which assumes no spatial structure within either the ESS or the WSS, 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 data of grey seals diets indicates that most seal eat little or no cod but a relatively few seals eat a high proportion of cod (Beck et al. 2007). Nevertheless, we lack the data to quantify the impact of these assumptions on cod population recovery. The last assumption is somewhat hotly debated and is discussed in terms of the uncertainty and bias in the diet data below.

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 (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 or WSS. Our estimates of cod biomass differ from the current assessments (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 1.8 times more cod in 1993, the year the coupling coefficient is estimated (Trzcinski et al (2006): 18,117 t, current model: 31,961 t), resulting in a much weaker interaction coefficient (q_a in equation 13 in Trzcinski et al. 2006). This change between studies emphasizes the importance of the interaction parameter on the estimate of mortality due to seal predation.

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. We provide the first estimates of total prey consumption by grey seals for the WSS. These estimates do not currently include grey seals from the small colonies in southwest Nova Scotia, as it is not clear if these colonies are used every year. There were 204 pups counted on Noddy and Flat islands in 2007 (Hammill et al. 2007), representing perhaps another 800 seals. Thus, our estimate may underestimate total grey seal consumption by approximately 6% if these seals forage only in WSS. It is not known if grey seals further south in New England forage in 4X. Our estimate of the relative impact of grey seals on the

WSS cod population is preliminary and should be viewed as illustrative until such time as estimates of diet of grey seals feeding in WSS are available.

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Table 1. The percentage of the Sable and Gulf and grey seal populations inhabiting the Eastern Scotian Shelf (ESS), (a), and Western Scotian Shelf (WSS), (b), by quarter. The Sable estimates are separated by 3 categories: young of the year (YOY), juveniles (males <10, females <6 years old) and adult males and females (n = 24, 43, 46 tracts, respectively from 105 seals). Estimates were derived from a state-space movement model (Breed 2008, Breed et al. in press). The Gulf population estimates are for combined ages (n = 54 individuals). Note: Gulf estimates are unchanged from Trzcinski et al. (2006).

		Quarter (%)			
Population	Category	1st	2nd	3rd	4th
(a)					
Sable	YOY	92	95	93	99
	Male	60	81	75	84
	Female	91	80	68	86
Gulf	All	39	29	1	8
(b)					
Sable	YOY	5	1	0	0
	Male	17	11	4	7
	Female	0	0	0	0
Gulf	All	1.6	2.8	0	0.2

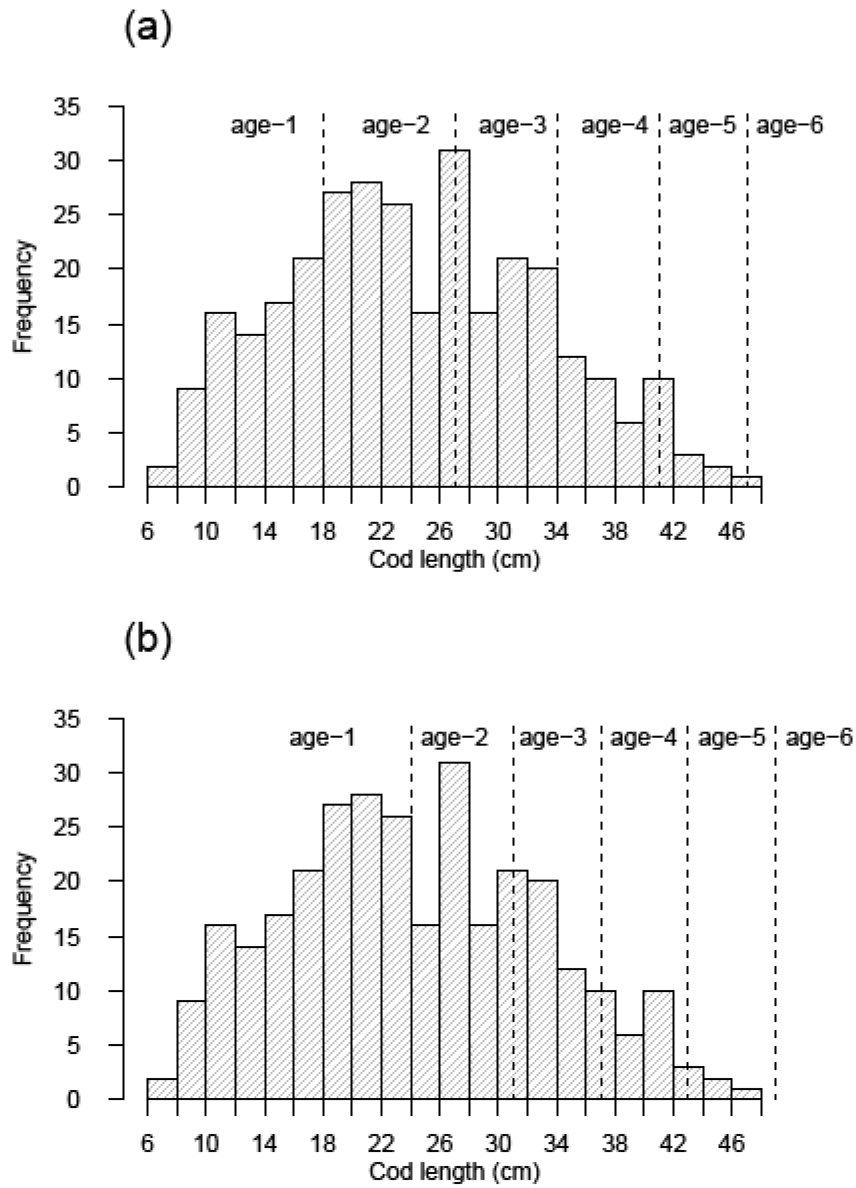

Figure 1. The frequency of cod lengths consumed by grey seals on the Eastern Scotian Shelf determined from otolith length (n=309). Dashed lines indicate age break points from (a) Trzcinski et al. (2006) and (b) this study.

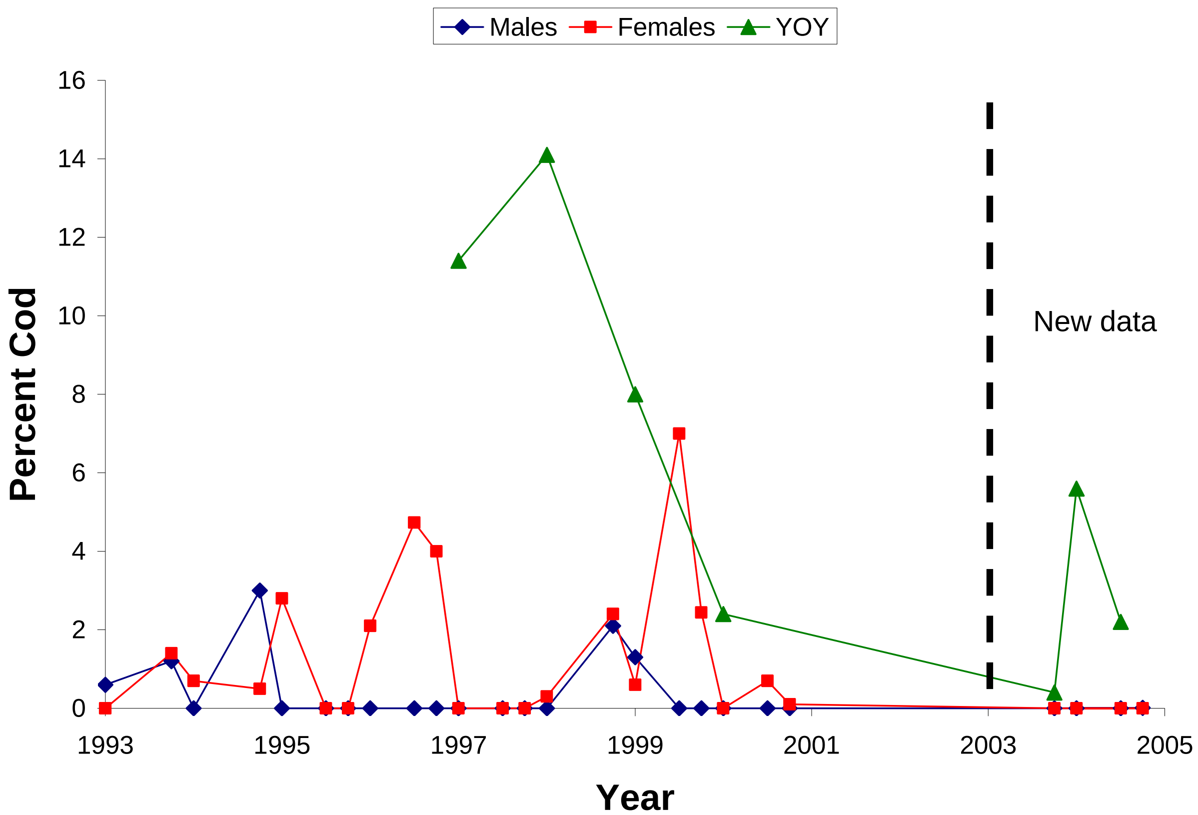

Figure 2. The percent cod in male, female, and young of the year (YOY) grey seal diet estimated from quantitative fatty acid signature analysis (QFASA). Values from 1993 to 2000 were used in Trzcinski et al. (2006). The values for 2003 and 2004 have been incorporated into the overall estimate used in this analysis.

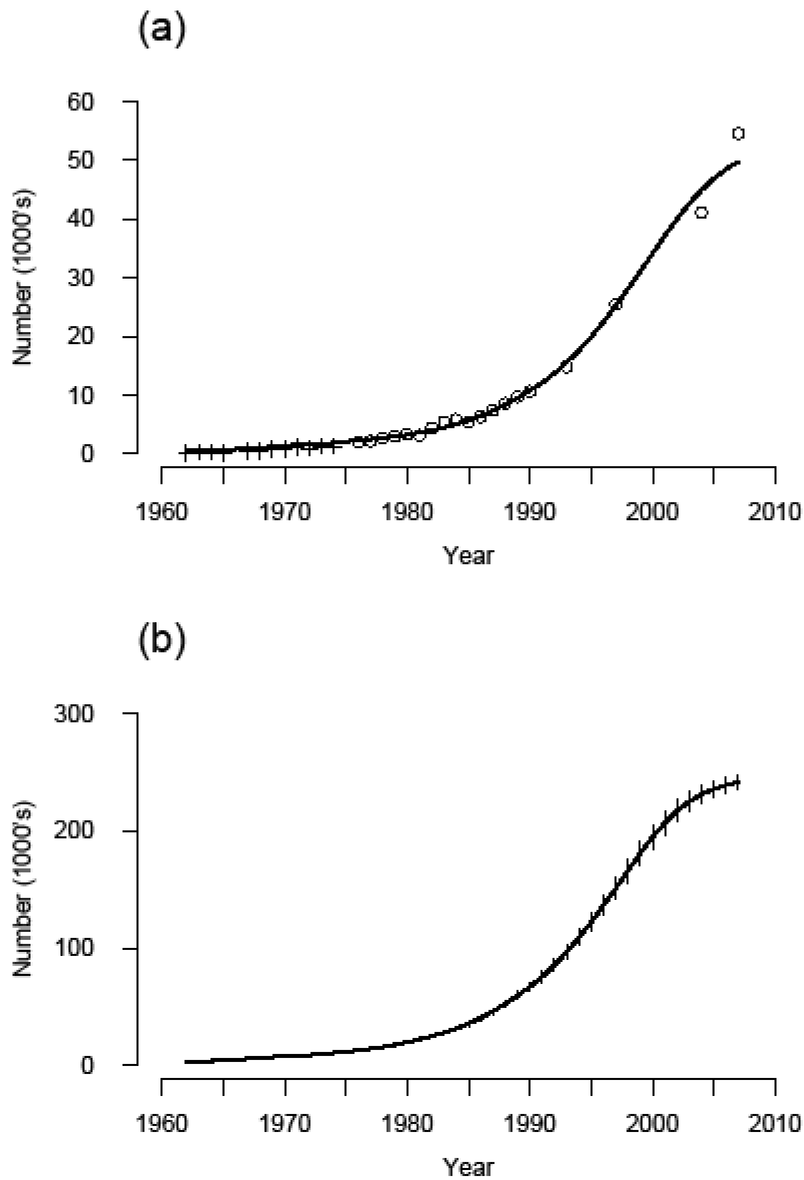

Figure 3. Census counts and model fit (solid line) to the pup production of the Sable Island grey seal population (a). Model estimates of total population size (b). Horizontal lines indicate the 95% C.I.

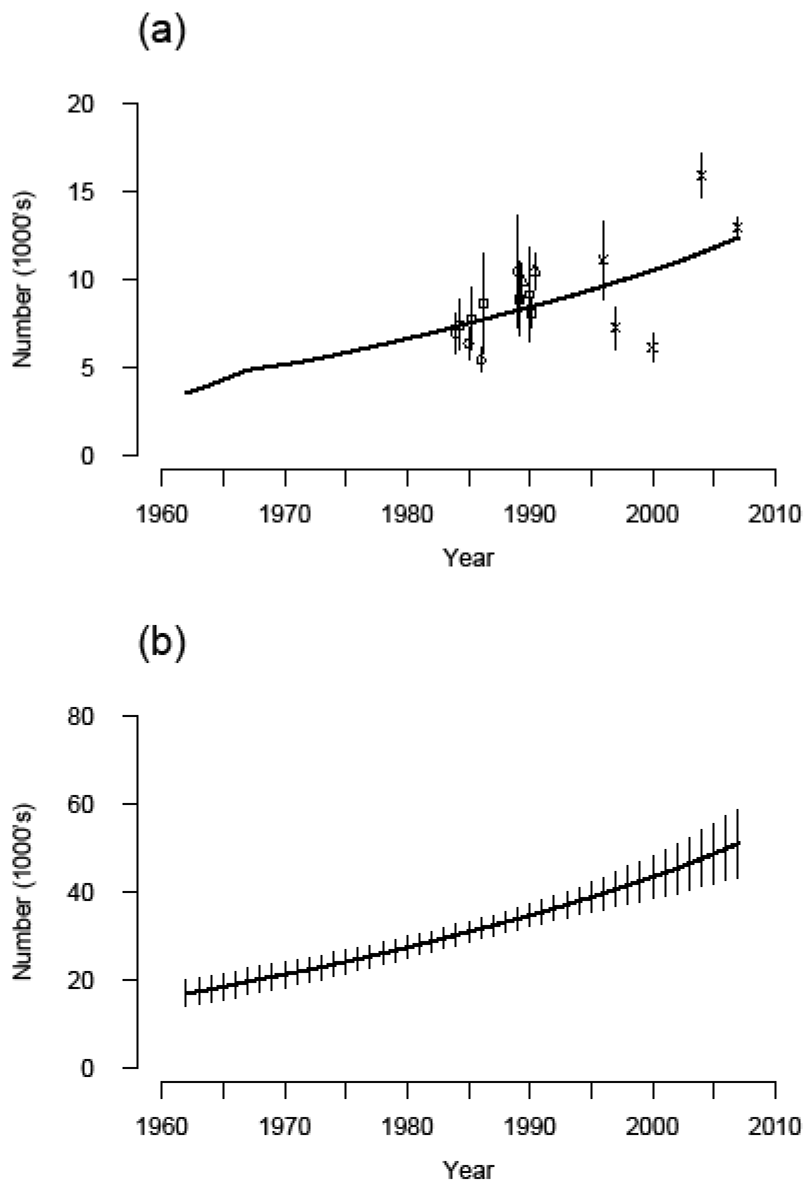

Figure 4. Census counts and model fit (solid line) to the pup production of the Gulf of St. Lawrence grey seal population (a). Model estimates of total population size (b). Horizontal lines indicate the 95% C.I.

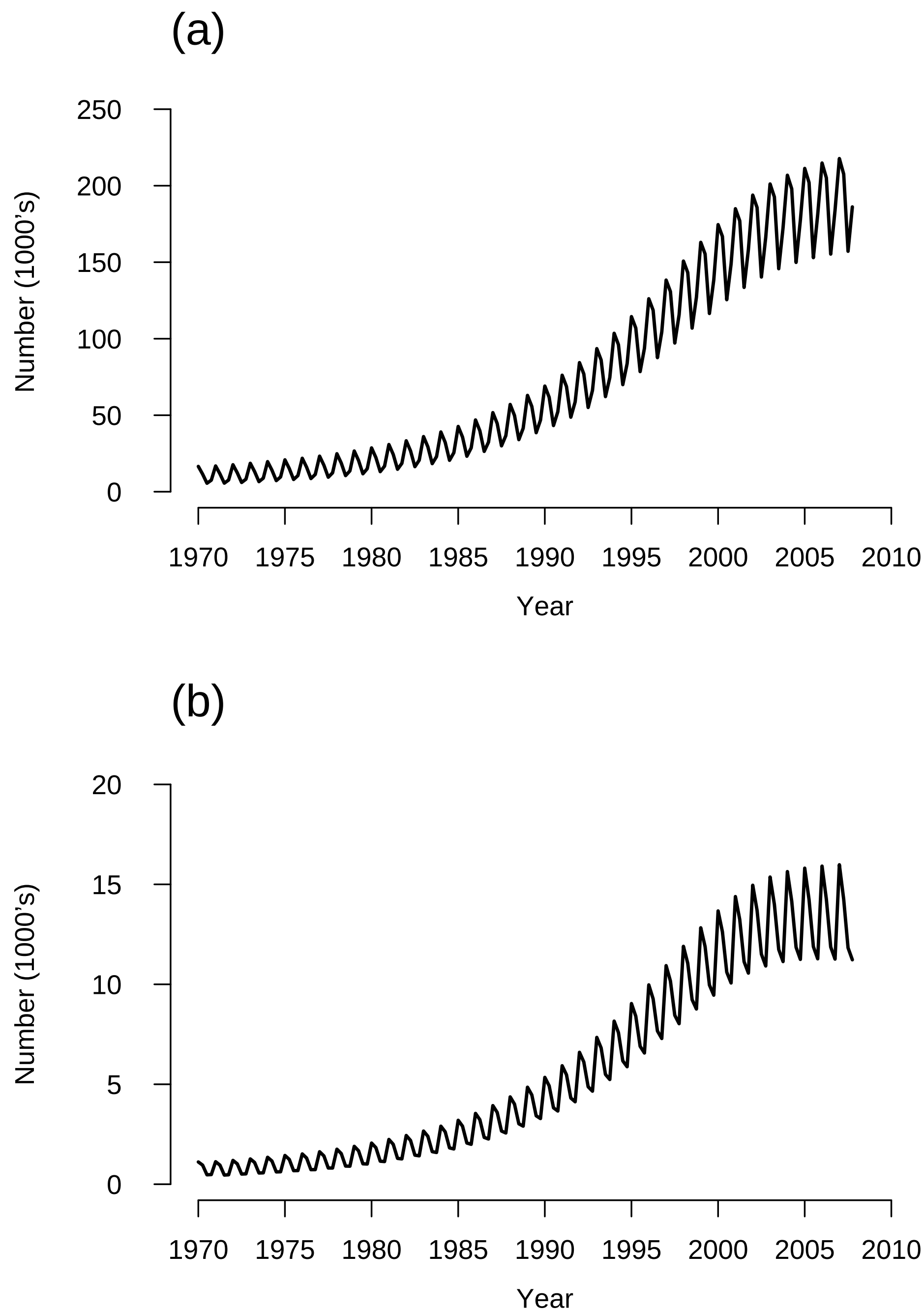

Figure 5. Estimated total number of grey seals on (a) the Eastern Scotian Shelf and (b) the Western Scotian Shelf accounting for population trends and immigration and emigration.

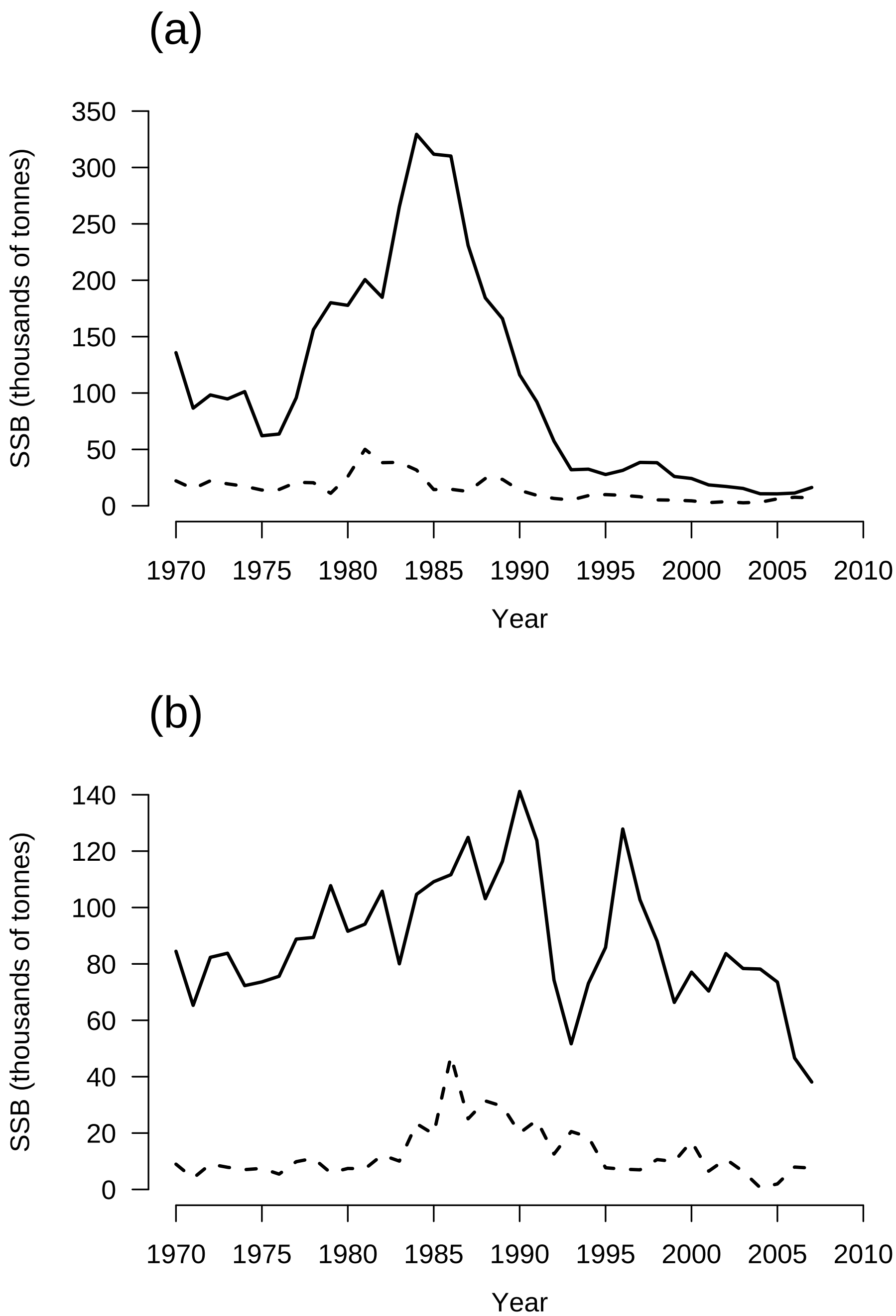

Figure 6. The estimated trends in (a) the Eastern Scotian Shelf cod spawning biomass (solid line) and the biomass of cod selected by seals (dashed line), and (b) the Western Scotian Shelf cod spawning biomass (solid line) and the biomass of cod selected by seals (dashed line).

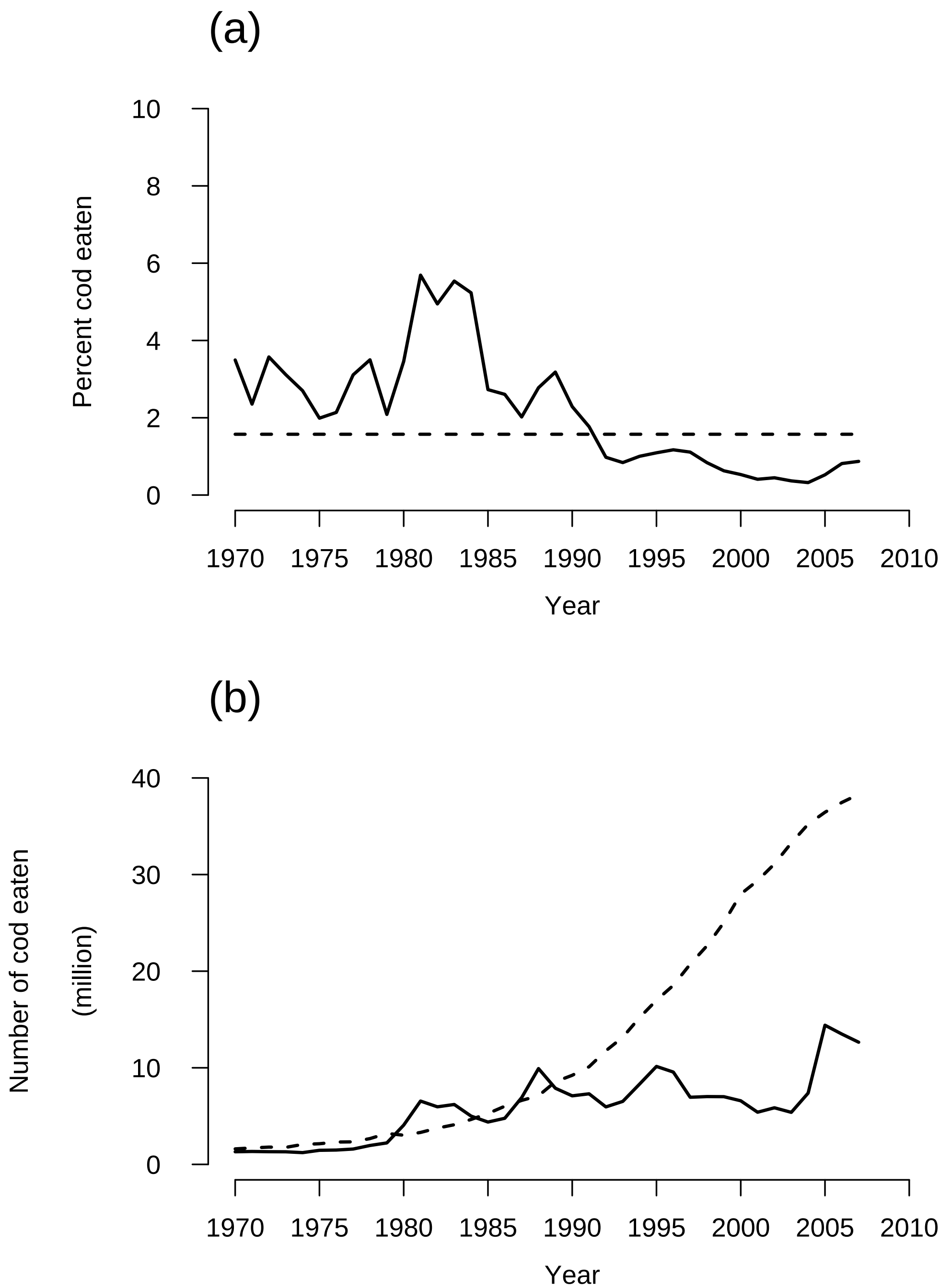

Figure 7. Results of the constant ration (dashed line) and the functional response model (solid line) for the percent cod in grey seal diet (a) and the numbers of cod consumed by grey seals (b) on the Eastern Scotian Shelf.

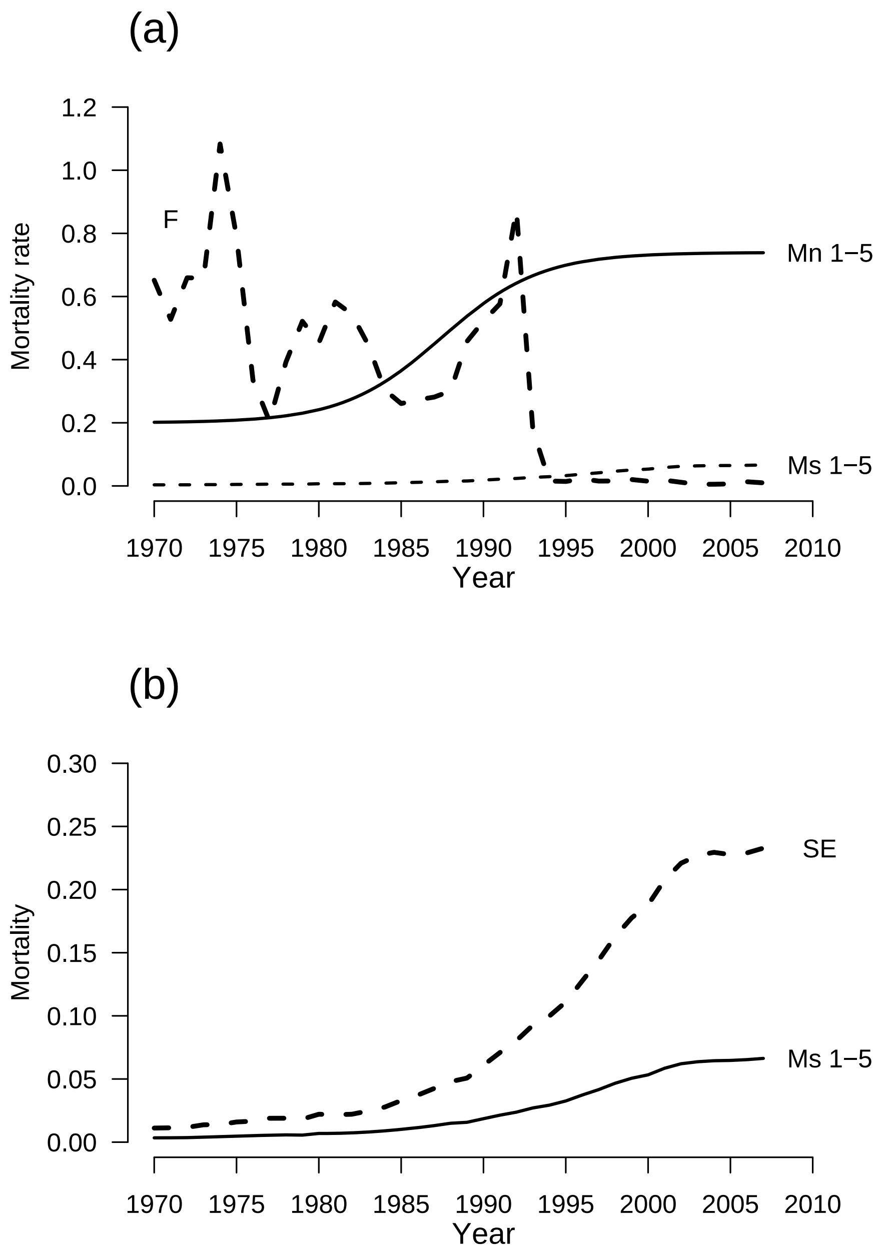

Figure 8. The instantaneous fishing mortality for fully selected fish (F, dashed line), estimated increased in natural mortality (Mn) for ages 1 to 5, and estimated trend in seal predation mortality (Ms) on ages 1 to 5 from the functional response model for cod on the Eastern Scotian Shelf, (a). The 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.

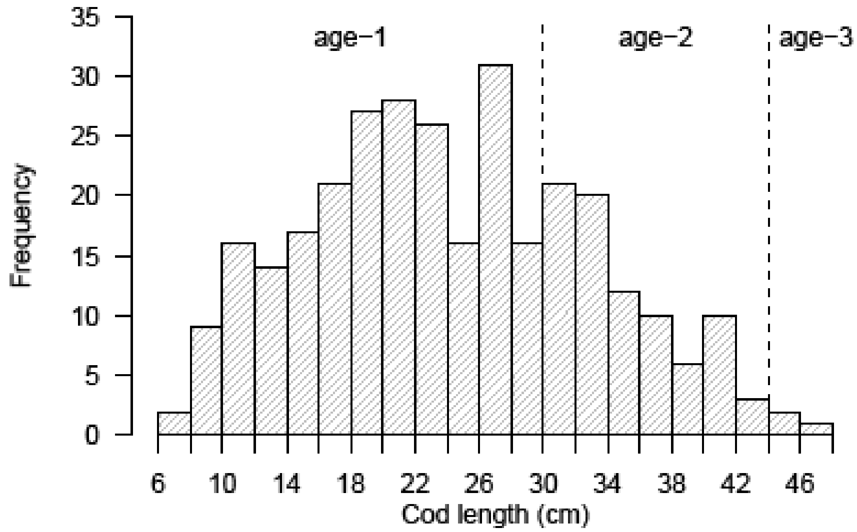

Figure 9. Cod length frequency reconstructed from otoliths sampled in scat were transformed into approximate ages using growth data from the Western Scotian Shelf cod. Dashed lines indicate age break points.

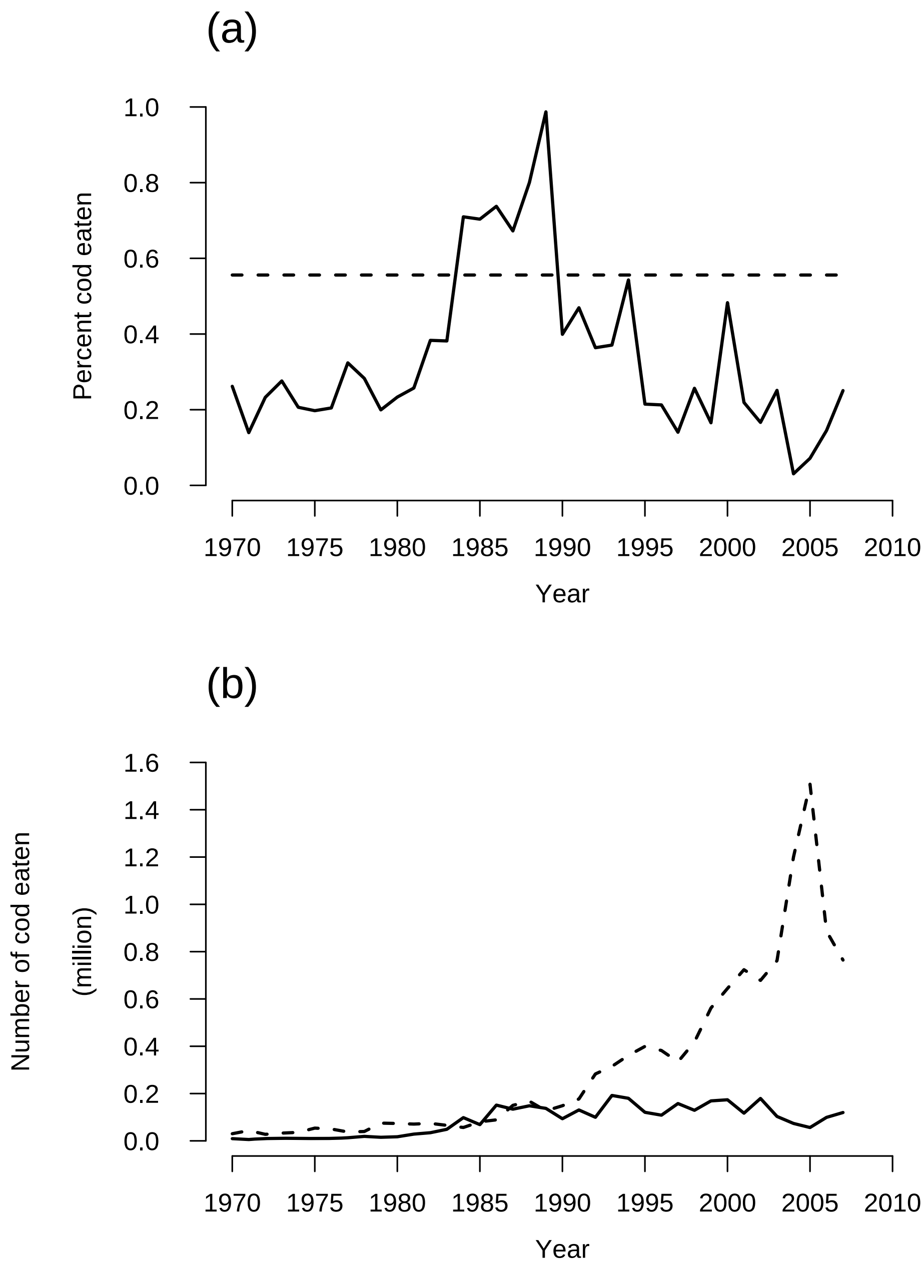

Figure 10. Results of the constant ration (dashed line) and the functional response model (solid line) for the percent cod in a grey seal diet (a) and the numbers consumed by grey seals (b) on the Western Scotian Shelf.

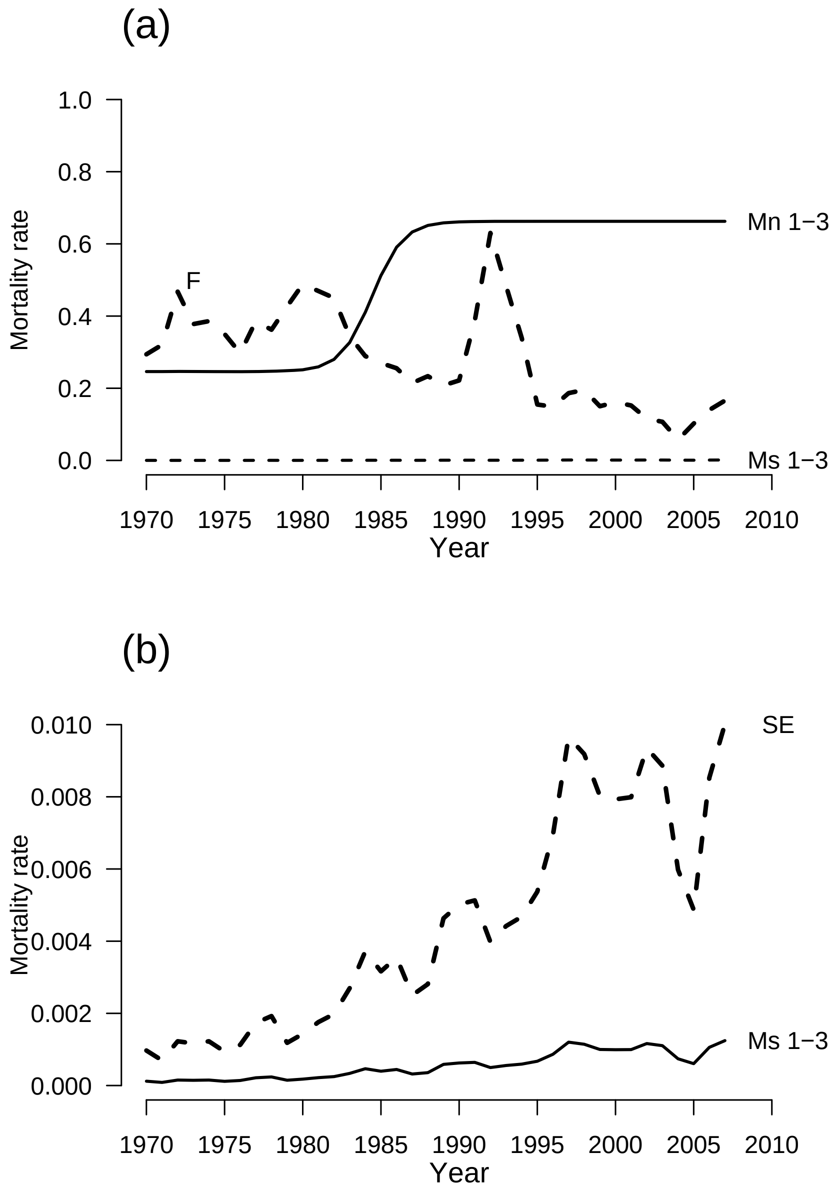

Figure 11. The instantaneous fishing mortality for fully selected fish (F, dashed line), estimated increased in natural mortality (Mn) for ages 1 to 3, and estimated trend in seal predation mortality (Ms) on ages 1 to 3 from the functional response model for cod on the Western Scotian Shelf, (a). The 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.