Covariation between grey seal (*Halichoerus grypus*) abundance and natural mortality of cod (*Gadus morhua*) in the southern Gulf of St. Lawrence

G.A. Chouinard, D.P. Swain, M.O. Hammill, and G.A. Poirier

Abstract: More than 10 years after the collapse of Atlantic cod (*Gadus morhua*) fisheries in Canada, the role of increased seal populations in the decline and lack of recovery of the stocks continues to be discussed. Using removals and abundance indices from synthetic populations, we found that sequential population analysis can uncover trends in natural mortality. We used this approach to examine variation in natural mortality (*M*) of southern Gulf of St. Lawrence cod. *M* increased from the late 1970s to the mid-1990s but declined slightly recently. Results were consistent with previous work indicating that *M* increased in the 1980s. Changes in estimated *M* for this cod stock matched fluctuations in grey seal (*Halichoerus grypus*) abundance. The increase in grey seal abundance from the late 1970s to the mid-1990s corresponded with the increase in estimated *M* of cod over this time period. The correspondence between seal abundance and *M* of cod supports the hypothesis that seal predation may be a cause of increased *M*. However, the diet information available suggests that seals consume mainly juvenile cod, whereas our evidence for an increase in *M* is for larger cod (ages 3 years and older).

Résumé : Plus de 10 ans après l'effondrement des pêches de morues franches (*Gadus morhua*) au Canada, on continue à discuter du rôle de l'augmentation des populations de phoques dans le déclin et l'absence de récupération des stocks. À l'aide de captures et d'indices d'abondance de populations synthétiques, nous avons découvert que l'analyse séquentielle de la population peut révéler les tendances de la mortalité naturelle. Nous avons utilisé cette méthodologie pour examiner la variation de la mortalité naturelle (*M*) chez les morues de la région sud du golfe du Saint-Laurent. *M* a augmenté de la fin des années 1970 jusqu'au milieu des années 1990 et a baissé un peu récemment. Ces résultats concordent avec des travaux antérieurs qui indiquent une augmentation de *M* durant les années 1980. Les changements dans la valeur estimée de *M* de ce stock de morues correspondent aux fluctuations de l'abondance des phoques gris. L'accroissement de l'abondance des phoques gris de la fin des années 1970 jusqu'au milieu des années 1990 correspond à une augmentation de la valeur estimée de *M* des morues durant la même période de temps. La correspondance entre l'abondance des phoques et la mortalité naturelle des morues appuie l'hypothèse selon laquelle la prédation par les phoques peut être la cause de la valeur accrue de *M*. Cependant, l'information disponible sur le régime alimentaire des phoques indique qu'ils consomment surtout des jeunes morues, alors que nos données indiquent qu'un accroissement de *M* se produit chez les morues plus grandes (âgées de 3 ans ou plus).

[Traduit par la Rédaction]

Introduction

Since the collapse of most of the Atlantic cod (*Gadus morhua*) fisheries off the east coast of Canada in the early 1990s, there has been considerable debate regarding the causes for their decline and subsequent lack of recovery. While it has been shown that increases in fishing mortality (*F*) played a major role in the collapse (Myers and Cadigan 1995; Sinclair and Murawski 1997; Shelton and Lilly 2000), some studies have also hypothesized that increases in the instantaneous rate of natural mortality (*M*) could have occurred during the same period (see review in Shelton and Lilly 2000).

Recently, Sinclair (2001) showed that *M* for cod in the southern Gulf of St. Lawrence was around 0.4 in the mid-1990s, about twice the levels previously assumed. His analysis suggested that *M* had started to increase in the early 1980s. This result has been incorporated in recent population reconstructions using sequential population analysis (SPA) by assuming that *M* doubled from 0.2 to 0.4 in 1986 (Chouinard et al. 2003).

Causes of this apparent increase in *M* are unknown. Possibilities include unreported catch, disease, toxins, starvation, parasitism, and predation. The possibility of unreported

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catch is unlikely. At the low spawning stock biomass occurring in the 1990s, about 20 000 t of unreported catch would be required to account for an apparent increase in M from 0.2 to 0.4 in the case of southern Gulf cod (G.A. Chouinard, unpublished data). It is unlikely that such a high level of unreported catch would have gone unnoticed in the absence of a directed cod fishery in the mid-1990s. There is no evidence for recent increases in disease, parasitism, or toxins. For northern Gulf cod, it has been suggested that cold environmental conditions in the early to mid-1990s may have resulted in increased M of cod as a result of poor growth and physiological condition (Lambert and Dutil 1997). Although there is some evidence for an effect of water temperature on growth of southern Gulf cod (Campana et al. 1995; Sinclair et al. 2002; Swain et al. 2003), growth and physiological condition in this stock declined in the late 1970s and early 1980s, well in advance of the onset of cooling in the late 1980s.

Harp (*Phoca groenlandica*) and grey seals (*Halichoerus grypus*) are predators of cod in the southern Gulf of St. Lawrence. Harp seals occur in the southern Gulf during late winter and early spring, a time when adult cod are overwintering outside the Gulf in the Sydney Bight area off the east coast of Cape Breton Island. Grey seals, on the other hand, are present year-round in southern Gulf waters and on the Scotian Shelf (Stobo et al. 1990; Lavigueur and Hammill 1993; Goulet et al. 2001), where they can co-occur with overwintering southern Gulf cod. Seals in Atlantic Canada have a varied diet and cod usually represent less than 20% of their diet (Hammill and Stenson 2000). Data on the diet composition of harp seals in the southern Gulf are limited, but the existing information suggests that consumption of cod from this stock is low (Beck et al. 1993; Hammill and Stenson 2002). However, cod can be an important item in the diet of grey seals in the southern Gulf of St. Lawrence (Hammill and Stenson 2002).

In other areas, detailed diet composition data have allowed removals of cod by seals to be incorporated into population assessment models (e.g., Mohn and Bowen 1996; Fu et al. 2001). Unfortunately, while there are estimates of consumption of cod by seals, the long time series of cod removals-at-age by seals required for these analyses do not exist for the southern Gulf of St. Lawrence. While these data are not available, there are relatively good estimates of the abundance of grey seals in Atlantic Canada (Mohn and Bowen 1996; Hammill and Stenson 2002; Bowen et al. 2003). Pup production provides indices of abundance for grey seal populations. Pup production on Sable Island has been increasing exponentially at an annual rate of 12.8%, from about 2000 animals in 1977 to 25 400 in 1997 (Bowen et al. 2003). A second large component of the grey seal population whelps primarily on the pack ice in the southern Gulf of St. Lawrence. Pup production in this area increased from 7200 in 1984 to 11 100 in 1996 and then declined rapidly to 7300 in 1997 and 5400 in 2000 (Hammill et al. 2003; Hammill and Stenson 2002). The recent decline in the southern Gulf pup estimates is likely due to increased pup mortality, a shift in pupping of females to areas outside the Gulf, or a combination of the two owing to poor ice conditions in recent years (M.O. Hammill, unpublished data).

In this paper, we explore the possibility that the increase in M of southern Gulf cod is a result of increased predation by grey seals. We obtain estimates of M in the southern Gulf stock for various time periods between the mid-1970s and 2001 and show that the trend in M corresponds closely to trends in the abundance of grey seals in the southern Gulf, consistent with the hypothesis that the increase in M of cod in the southern Gulf is a result of increased predation by grey seals.

Methods

Estimating M from SPA

Conventional age-structured assessment models typically assume that M is known (see review in Megrey 1989). Because studies to estimate M are rarely carried out, the value used for M in these models is usually an assumption rather than an empirical estimate. The principal reason for making an assumption about M rather than attempting to estimate it is that it can be confounded with other parameters of interest such as F, population size, and catchability coefficients. However, Schnute and Richards (1995) showed, using simulation-estimation techniques, that it is feasible to estimate M in catch-age models. Similarly, Fu and Quinn (2000) found that interannual variation in M could be estimated in a stock assessment model of *Pandalus borealis* using the AD model builder (ADMB) methodology.

In this study, we estimated trends in M as part of the "calibration" of SPA. SPA produces estimates of population abundance by adding up fish catches along cohorts or year classes while adjusting for M. The basic population equation used in the SPA is as follows:

$$(1) \qquad N_{a,t} = N_{a+1,t+1}\, e^{M_{a,t}} + C_{a,t}\, e^{M_{a,t}/2}$$

where $N_{a+1,t+1}$ is the number of survivors at age a + 1 in year t + 1, $C_{a,t}$ is the catch in numbers at age a in year t, and M is the instantaneous rate of natural mortality. The catch is assumed to occur in midyear and measured without error, the usual assumption in many cod assessments. Starting estimates of the survivors in the last year of analysis are needed to begin SPA. Parameter estimates are obtained by calibrating the SPA using population abundance indices (e.g., mean catch rates in a research survey). Calibration involves finding the parameter estimates that produce the best match between the SPA estimates of population size and the population abundance indices. We used the ADAPT framework (Gavaris 1988) to calibrate SPA. The ADAPT software allows for the estimation of M in addition to providing estimates of the survivors at age in the terminal year and catchability coefficients (q) at age for the population abundance indices. These parameters are estimated using nonlinear least squares by minimizing the following objective function:

$$(2) \qquad \sum\nolimits_{a,t,i} [\ln(I_{a,t,i}) - \ln(q_{a,i} N_{a,t})]^2$$

where $I_{a,t,i}$ is the abundance index at age a in year t for abundance index i, $q_{a,i}$ is the catchability coefficient at age a for index i, and $N_{a,t}$ is the number of survivors at age a at the beginning of year t.

We first conducted a simulation study to investigate the feasibility of estimating trends in M using the ADAPT software. To limit the number of parameters and to reduce the possibility of spurious results owing to “year effects” (i.e., interannual fluctuations in catchability), we investigated the reliability of estimating M for blocks of years (periods varying from 5 to 9 years) rather than individual years.

We generated three synthetic populations with known underlying patterns of M. These synthetic populations, each comprising 13 age-classes, were generated by defining an initial (1st year) population and then making a forward projection over 31 years using randomly selected F (0.2 ± 50%), randomly selected recruitment (20 000 ± 10% or 20%), a constant exploitation pattern by age, and the following three M profiles: $M = 0.2$ from year 1 to 14 and then 0.4 for years 15–31, $M = 0.2$ from year 1 to 3 and then increasing in gradual increments of 0.02 to reach 0.4 in year 14 and remaining at 0.4 thereafter, and $M = 0.2$ for years 1–10, $M = 0.4$ for years 11–23, and $M = 0.2$ for years 24–31.

We used two different catchability profiles (constant for all years) to construct two “exact” survey indices. These abundance indices were then randomly perturbed (30% coefficient of variation for each index). We used ADAPT to estimate the population parameters with the catch-at-age calculated in generating the population and the perturbed indices. Standard errors of the parameter estimates are obtained using the covariance matrix (Gavaris 1988). In addition to the usual parameters (terminal population estimates and catchability coefficients for the abundance indices), we used ADAPT to estimate M for equal periods of 5–9 years (one value for each 5- to 9-year period). The periods were defined starting with the terminal year (e.g., for 5-year periods: years 27–31, 22–26, 17–21, 12–16, and 7–11). A value for M was assumed rather than estimated for the 3- to 6-year period at the beginning of the time series (M_{initial}). The sensitivity of the estimated trend in M to the value assumed at the beginning of the time series was examined by conducting analyses assuming $M_{\text{initial}} = 0.1$, 0.2, and 0.4. Using the different assumptions of M_{initial} resulted in a scaling up or down of the estimated M; however, the trends in M were similar. Because the trends in estimated M were not sensitive to this assumption, we used the analyses assuming $M_{\text{initial}} = 0.2$, as this was the value for M assumed in earlier cod assessments based on studies conducted prior to 1980 (see Sinclair 2001). Besides the estimation of M by time periods, the rest of the calibration model was similar to that used in the assessment of southern Gulf of St. Lawrence cod (Chouinard et al. 2003).

For each of the three populations generated using the different M profiles, the calibration of the population model using ADAPT was repeated 500 times. At each iteration, the exact abundance indices were randomly perturbed and the ADAPT calibration repeated. Finally, we compared the trends in the estimates of M with those originally used to generate the synthetic populations.

Natural mortality for southern Gulf of St. Lawrence cod and grey seal population estimates

As in the simulation study, we estimated M for the southern Gulf of St. Lawrence cod stock in blocks of 5–9 years. Data for the period 1971–2002 were available. The formulation of the population model was similar to that used in the most recent assessment of this stock (Chouinard et al. 2003). In summary, eight population abundance indices were used in the SPA calibration: a research vessel abundance index (a = 2–10, t = 1971–2002), an otter trawl catch rate series (a = 5–12, t = 1982–1993), and six sentinel survey indices using various gear types and mesh sizes (various ranges for a, t = 1995–2002 or 1996–2002). Sentinel surveys are stock abundance monitoring activities conducted by the fishing industry. All observations were given equal weight. The relationship between abundance indices and population numbers was assumed to be proportional except for the otter trawl catch per unit of effort index where a trend in catchability was estimated:

$$(3) \qquad I_{a,t} = (k_a \tau_a^{T-T_1}) P_{a,t}$$

where I is the catch rate index at age a in year t, k is the catchability coefficient at age a, τ is the trend coefficient, T is time, and P is the population abundance at age a and time t.

Fishing mortality on the oldest age was set to the average for the two previous age groups. As in the simulation study, calibration was achieved by minimizing the sum of squares of the objective function given by eq. 2.

In addition to estimating M for periods of 5–9 years, $q_{a,i}$ and the trend coefficients by age for the catch per unit of effort index (τ_a), $N_{3,2003}...N_{14,2003}$ and $N_{15,2000}...N_{15,2003}$, were estimated. Given the results obtained in the simulation study (see previous section), M was assumed to be 0.2 in the 2- to 8-year time period at the beginning of the time series (M_{initial}). We compared the fit and the population estimates of the various population models described above with the model used in the 2003 assessment where M is set equal to 0.2 for the period 1971–1985 and 0.4 for 1986–2002 (Chouinard et al. 2003). For completeness, we also compared the results of the variable-M models with the results obtained using constant M. Historically, assessment of this cod stock used a constant M of 0.2 (Sinclair 2001). In our analyses, we investigated models with constant M of 0.1, 0.2, 0.3, 0.4, and 0.5. In total, between 85 and 91 parameters were estimated in the models and there were 732 observations. We compared the fit of the various models using the corrected Akaike information criterion (AIC_c) calculated as described in Burnham and Anderson (1998). The differences between the AIC_c value for each model and that for the model with the lowest AIC_c (ΔAIC_c) provide a means of ranking model fits. If a particular model has $4 < \Delta\text{AIC}_c < 7$, there is evidence that the model is not the best and a value of $\Delta\text{AIC}_c > 10$ is considered very strong evidence that the model is not the best (Burnham and Anderson 1998).

Grey seal population estimates for the Gulf of St. Lawrence were obtained using the model described in Mohn and Bowen (1996) but with reproductive rates from data collected in the Gulf of St. Lawrence in the 1980s and 1990s (Hammill and Gosselin 1995). The model was initially fit to data available to Mohn and Bowen (1996) to verify model consistency. It was then fit in two steps to a larger data set that included more recent estimates of grey seal pup production in the Gulf of St. Lawrence. The first step included fitting the model to the increasing series of pup production estimates from 1984 to 1996 by adjusting initial population size and adult and pup mortality. The model was then fit to the pup production estimates from 1997 and 2000 by adjusting pup mortality for 1997 and onwards.

Finally, we compared the estimated trend in grey seal abundance in the Gulf with the trend in M estimated by SPA. For each model, we computed Spearman's coefficient of rank correlation between the M estimates and the average seal abundance during the corresponding period to provide an indication of association.

Results

Estimating *M* from SPA

The simulations indicated that trends in M could be reliably estimated as part of the SPA calibration (Fig. 1). The estimation uncovered the general trends in underlying M for the three simulated populations for all time period lengths. Where abrupt changes in M were used in generating the populations (e.g., a doubling or halving of M in one year) (Figs. 1*a* and 1*c*), estimates of M obtained from the 500 replicates were generally close to the true value. However, where a gradual increase had been imposed (Fig. 1*b*), although the general trend was revealed, the estimates of M in the period of increase were lower than the average true M during the period of increase.

Natural mortality for southern Gulf of St. Lawrence cod and grey seal population estimates

All of the population models with parameter estimates for M converged. The mean squared error (MSE) provides an estimate of the goodness of fit for these models. Overall, our analyses resulted in a slight reduction (1%–7%) in MSE (Table 1) over the model used in the assessment of the stock, which assumed a sudden increase in M (Chouinard et al. 2003). However, there was a greater than 15% reduction in MSE relative to models that assumed a constant M, the usual assumption in earlier stock assessment of this resource. The ΔAIC_c statistics, which take into account the difference in the number of parameters estimated, indicated that the model where M was estimated in periods of 7 years provided the best fit (Table 1). All of the models where M was estimated gave lower ΔAIC_c than the assessment model where a sudden change in M is assumed. The ΔAIC_c for the models assuming constant M were large relative to that of the other models and their results are not considered further.

Some high correlations ($r = -0.6$ to -0.8) occurred between estimates of M and q, mainly for the research vessel index, which covers the entire time series. Although M and q were closely correlated, the analyses consistently showed similar time trends in M despite using different time periods. In addition, the patterns of q by age for the various abundance indices, including the research vessel series, were similar between analyses estimating M for various time periods and between these analyses and the model used in the assessment (Fig. 2). As expected, different values of estimated M resulted in a scaling up or down of the catchability coefficients (higher estimates for M result in higher estimates of population size and thus lower estimates of catchability). Time trends in population abundance and F were also generally similar between our analyses and the standard assessment model (Fig. 3), although population abundance estimates were higher in the 1975–1990 period in most of the analyses where M was estimated. Fishing mortality estimates (ages 7+, weighted) during the period 1989–1992 were more than double the levels in the previous 4 years (1985–1988: $F = 0.26$ to 0.36; 1989–1992: $F = 0.64$ to 0.76). This is similar to the trends estimated in the stock assessment where M is not estimated. Estimated M increased progressively from values in the range of 0.25 to 0.30 in the late 1970s to approximately double that (0.45–0.56) in the late 1980s and early 1990s followed by a small decrease to values in the range of 0.34–0.39 in the late 1990s (Fig. 4).

Estimates of grey seal abundance from the Gulf of St. Lawrence showed a continuous increase from the early 1970s to the late 1990s (Fig. 4). The population is estimated to have declined slightly from 1997 to 2000 in response to the decline in pup production in the southern Gulf. Changes in estimated M matched estimated variation in the abundance of grey seals. The general increase in grey seal abundance from the late 1970s to the mid-1990s corresponded to the gradual increase in estimated M over this time period. Similarly, the recent decline of the component of the grey seal population that reproduces in the Gulf of St. Lawrence was matched by a decline in estimated M (Fig. 4). Spearman rank correlation indicated a significant ($\alpha = 0.05$) positive association between estimated M and average seal abundance for the periods for models using 5- and 6-year periods (Fig. 4). The usefulness of this statistic was limited for the other models because there were only three and four observations. Significance would have required complete correspondence of the ranks.

Discussion

Using simulation-estimation studies, Schnute and Richards (1995) and Fu and Quinn (2000) showed that variation in M could be estimated in population models. In our analyses, the simulation exercise also suggested that trends in M can be recovered through the calibration of SPA using the ADAPT framework. Similar to most population models, our analysis assumed that q at age is constant over time. This is a reasonable assumption for research and sentinel surveys because survey protocols and gear are standardized.

Schnute and Richards (1995) found that estimation models performed better when there was a reasonably reliable abundance index such as those produced from well-planned research surveys. For southern Gulf of St. Lawrence cod, the research survey is the main index of abundance and has been conducted continuously for 32 years following a stratified random design using standard methods (Hurlbut and Clay 1990). The survey area extends to shallow waters and contains little untrawlable area. The coefficients of variation of the research survey abundance indices are low, ranging from 10% to 25% for the most common age groups (Chouinard et al. 2003). Similarly, several other abundance indices derived from sentinel surveys that have been conducted since the mid-1990s have followed standardized methods. In our synthetic population analyses, the exact abundance indices were perturbed using a coefficient of variation of 30% so that input data would be more variable than those used in the assessment of cod in the southern Gulf of St. Lawrence. This should provide a conservative evaluation of the technique.

Fig. 1. Estimates of *M* from the simulation experiment for the three synthetic populations (*a*, *b*, and *c*) based on 500 bootstrap runs of the ADAPT framework. Box plots show the distribution of estimates of *M* for each time period; the line within the box marks the median, the lower and upper boundaries of the box show the 25th and 75th percentile, respectively, error bars below and above the box indicate the 10th and 90th percentiles, and circles show the extreme values. The line indicates the value of *M* used to generate the synthetic populations.

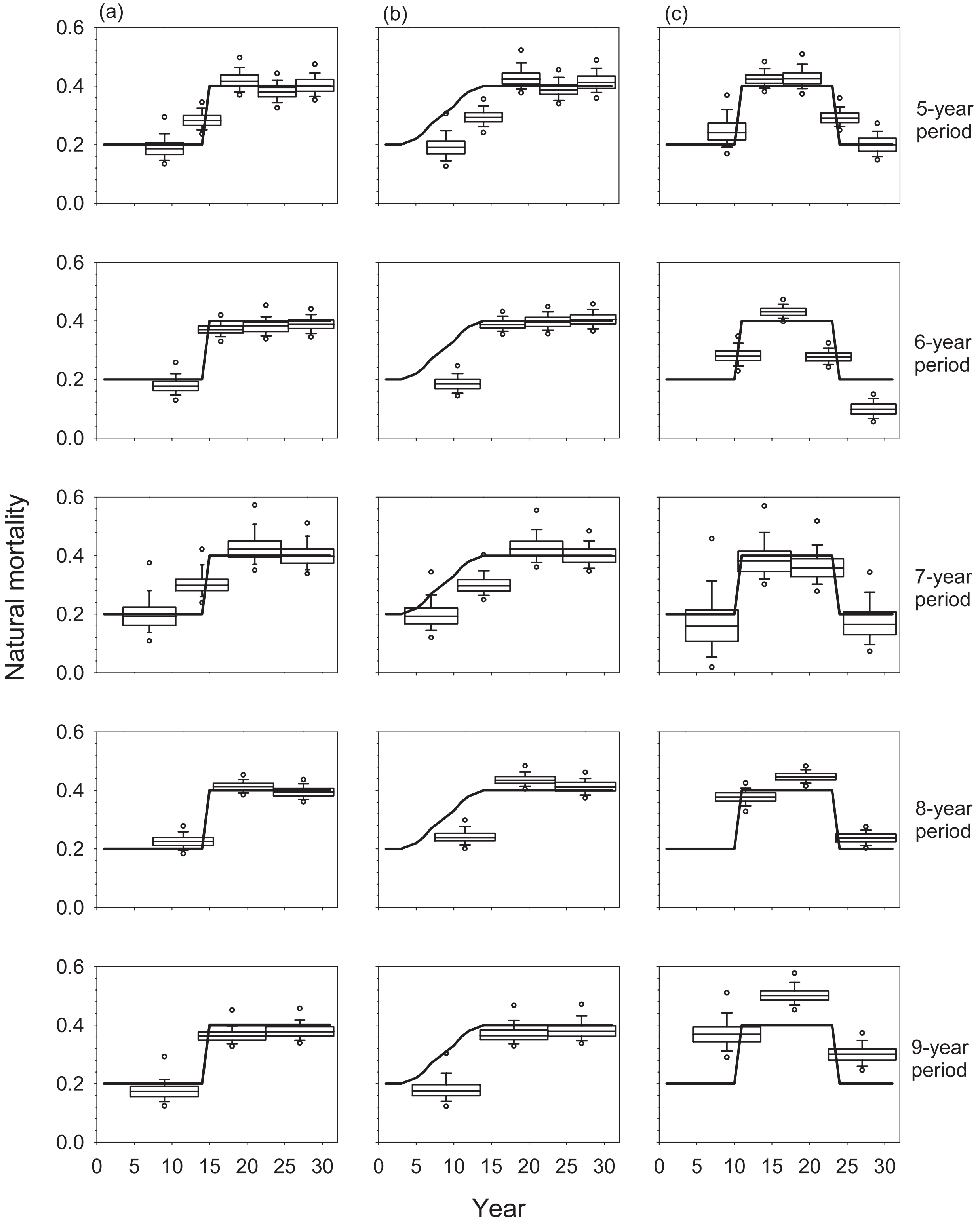


Table 1. Number of parameters (*P*), number of estimates of *M*, MSE, and ΔAIC_c for the population models for southern Gulf of St. Lawrence Atlantic cod (*Gadus morhua*).

Model	*P*	*M* estimates	MSE	ΔAIC_c
Estimates of *M* in 5-year periods	91	6	0.182	27.47
Estimates of *M* in 6-year periods	90	5	0.183	30.01
Estimates of *M* in 7-year periods	89	4	0.176	0.00
Estimates of *M* in 8-year periods	88	3	0.181	19.05
Estimates of *M* in 9-year periods	88	3	0.188	46.83
Assessment ($M = 0.2$ from 1971 to 1985, $M = 0.4$ from 1986 to 2002 (Chouinard et al. 2003))	85	0	0.190	50.25
Constant $M = 0.1$	85	0	0.230	190.10
Constant $M = 0.2$	85	0	0.216	144.13
Constant $M = 0.3$	85	0	0.210	123.51
Constant $M = 0.4$	85	0	0.213	133.89
Constant $M = 0.5$	85	0	0.227	180.49

These analyses also assumed that catch-at-age was measured without error, as is the case in this and most other cod assessments.

Estimates of *M* for southern Gulf of St. Lawrence cod followed a similar pattern regardless of the block size (5–9 years) used to estimate *M*: *M* increased from the late 1970s to the early 1990s and then declined in the late 1990s. The consistency of these results suggests that the patterns uncovered are not spurious (Fu et al. 2001). In addition, the fits of all of the models using a constant *M* were significantly poorer than those where an increase in *M* was either assumed or estimated.

The first estimate of *M* in our study (6-year time period from 1973 to 1978) was considerably lower than that obtained using other time blocks in the same period. The reasons for this difference are unclear but the larger confidence intervals indicated that it was a less precise estimate. Sinclair (2001) noted that survey estimates of total mortality (*Z*) produced a negative estimate for 1977, which is contained in this period.

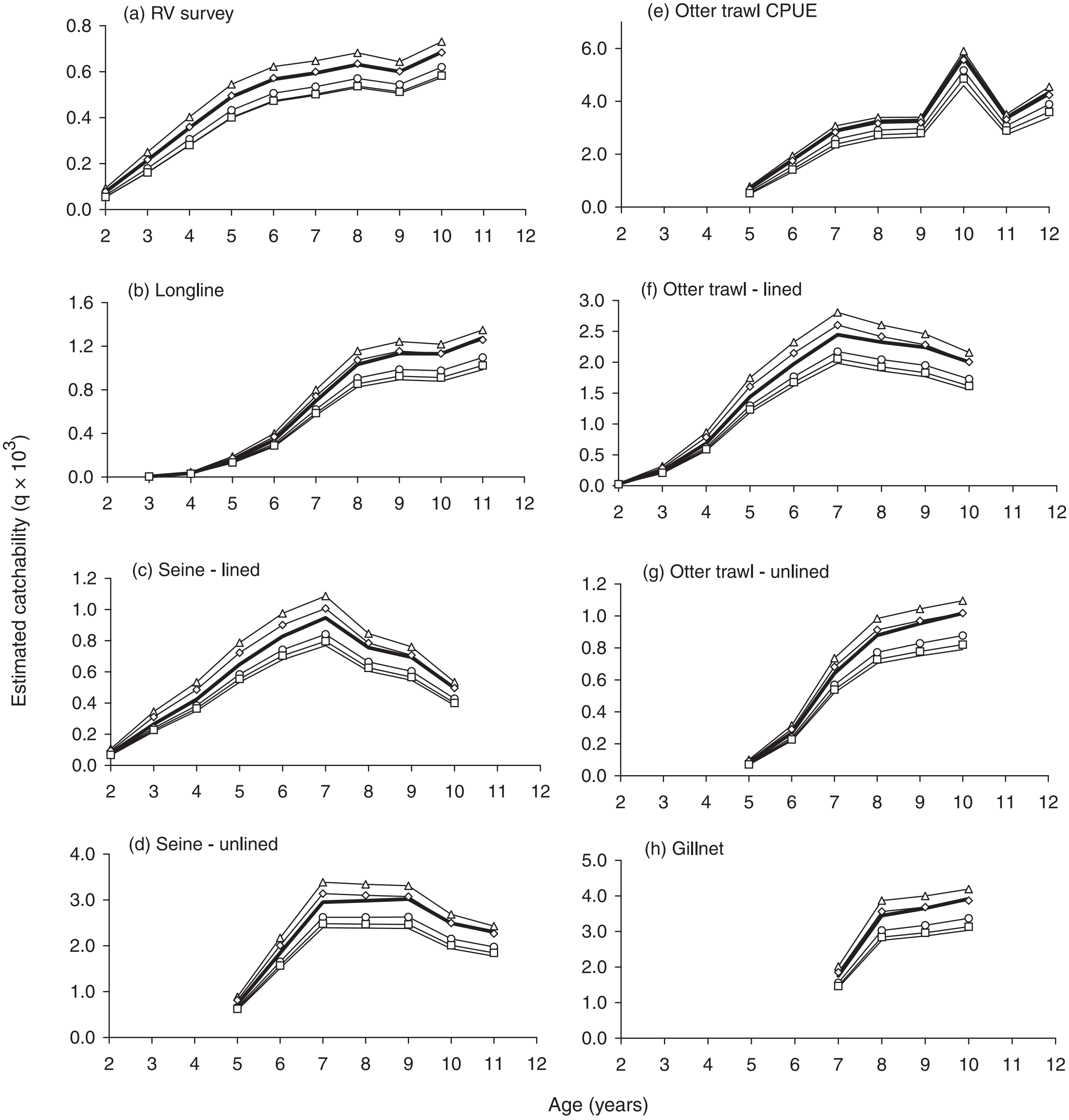
Our estimates of *M* in the mid-1990s for southern Gulf of St. Lawrence cod correspond well to Sinclair's (2001) estimate of *M* of about 0.4 in that period, using a modified catch curve analysis of the survey data. As well, the estimates of *M* from the SPA showed a trend similar to that of the residuals from a regression of *Z* on an index of fishing intensity (Sinclair 2001). To incorporate the increase in *M*, recent assessments of the stock (e.g., Chouinard et al. 2003) assumed a sudden doubling of *M* from 0.2 to 0.4 in 1986. This is ecologically unlikely and a gradual increase in *M*, as suggested by our analyses, would be more realistic.

Since the first closure of the fishery in the early 1990s, high *M* of adult cod has been one of the factors impeding the recovery of the southern Gulf cod stock from its collapse. The close correspondence between the estimated trends in the abundance of the Gulf of St. Lawrence component of the grey seal population and estimated *M* of cod supports the hypothesis that grey seal predation may be a cause of the increased *M* of cod in the southern Gulf of St. Lawrence. A difficulty with this hypothesis is that diet analyses suggest that grey seals feed primarily on small cod (Hammill and Stenson 2002), whereas evidence presented here and elsewhere (Sinclair 2001) indicates an increase in *M* of adult cod.

As in most other studies of pinniped diets (e.g., Murie and Lavigne 1985; Croxall 1993; Bowen 2000), estimated diet composition of seals in the Gulf of St. Lawrence is based on the hard body parts found in the digestive tracts and faecal material of seals. For example, the conclusion that the cod eaten by seals are mainly juveniles is based on the size distribution of cod otoliths recovered from seal stomachs (Hammill and Stenson 2002). This approach assumes that the hard parts recovered from seal stomachs are representative of the species composition and size distribution of prey consumed. However, selective rejection of fish heads has been suggested to occur in a number of seal species (Pitcher 1980; Lunneryd 2001; Moore 2003), and fishermen often report observations of seals feeding on large cod, consuming only the belly (including the energy-rich liver). This "belly-biting" has been documented for harp seals off Newfoundland (Fu et al. 2001). On the other hand, there is evidence from faecal samples of grey seals taking large cod (>40–90 cm; Bowen et al. 1993; Hammond et al. 1994*a*, 1994*b*), indicating that seals do not always consume only the soft parts of large fish. A link between grey seal abundance and the *M* of adult cod would require that grey seals frequently do not consume the head of large cod (>35 cm). Studies to determine the frequency of this behaviour should be encouraged. Alternative methods, such as fatty acid analyses (Iverson et al. 2004), may also lead to improved estimates of the diet composition of seals, free of the possible biases in diet reconstructions based on the hard parts found in digestive tracts and faeces.

Most estimates of consumption of southern Gulf cod by seals (Hammill and Stenson 2002) are lower than the amount required to account for the estimated increase in *M*. Estimated consumption by seals depends on their estimated population abundance, distribution, energy requirements, and diet composition. Distribution, energy requirements, and diet composition of seals can vary considerably both geographically and seasonally (Shelton et al. 1997). Diet samples are often collected in coastal areas, and it is assumed that diets in offshore areas are similar, which may not always be the case (Stenson et al. 1997). Most grey seal diet

Fig. 2. Estimated catchability (*q*) at age for the various abundance indices obtained from the population models for southern Gulf of St. Lawrence Atlantic cod (*Gadus morhua*) where *M* was estimated for periods of 5–9 years (circles, 5 years; triangles, 6 years; diamonds, 7 years; squares, 8 years; thin line, 9 years) and from the most recent assessment (thick line) of the stock (Chouinard et al. 2003). RV, research vessel; CPUE, catch per unit effort.



samples for the southern Gulf of St. Lawrence are summer samples from inshore areas (e.g., the Northumberland Strait) where cod are rare (Hammill and Stenson 2002) and diet information is lacking in the main areas of cod distribution (Bowen et al. 1993). Thus, consumption of cod by seals may currently be underestimated owing to seasonal and spatial biases in diet sampling and possible "belly-biting".

Previous analyses of the impact of seal predation on cod in other areas have estimated the removals-at-age of cod by seals based on diet analyses and incorporated these removals in population models (e.g., Mohn and Bowen 1996; Fu et al. 2001). However, for several stocks, attempts to incorporate estimated seal consumption of cod in population models have resulted in inconsistent results. For example, Shelton

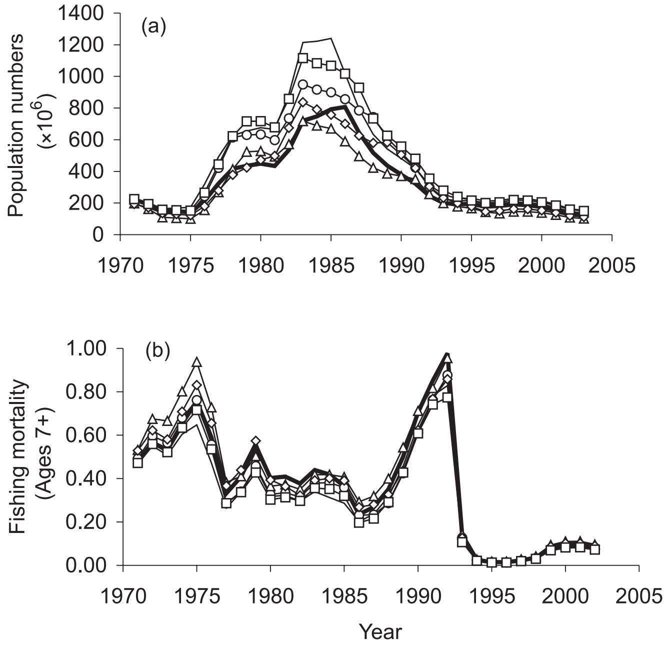


Fig. 3. (*a*) Population abundance and (*b*) *F* trends obtained from the population models for southern Gulf of St. Lawrence Atlantic cod (*Gadus morhua*) where *M* was estimated for periods of 5–9 years (circles, 5 years; triangles, 6 years; diamonds, 7 years; squares, 8 years; thin line, 9 years) and from the most recent assessment (thick line) of the stock (Chouinard et al. 2003).

and Lilly (2000) reported that estimates of cod consumed by seals were lower than the estimated "missing" fish for northern cod of ages 4 and 5. They also suggested that the discrepancy could be caused by seals feeding only on soft parts when consuming older cod.

We have focused on the congruent trends between *M* of adult cod and abundance of the Gulf grey seal herd. Grey seals from the Sable Island herd also occur in the Sydney Bight area where they may feed on southern Gulf cod in winter. In addition, while tag recoveries of Sable Island seals indicate that most of these animals remain on the Scotian Shelf throughout the year, some animals have a tendency to move into the Gulf. Most of these animals migrate to the northern Gulf near Anticosti Island or into the St. Lawrence Estuary during late spring and exit the Gulf in fall (Stobo et al. 1990). Abundance trends were parallel between the two herds until the mid-1990s. Since then, pup production has continued to increase on Sable Island, whereas it has declined by over 50% in the Gulf (Hammill and Stenson 2002; Bowen et al. 2003). The decrease in pup production is estimated to have caused a decline in the population in the Gulf (Hammill and Stenson 2002; this analysis). Our analysis suggests that the decline of the grey seal population in the Gulf between 1996 and 2000 was smaller than that estimated by Hammill and Stenson (2002). However, there is a similar correspondence to variation in estimated *M* irrespective of the series used. Finally, harp seals could also be important predators of cod in the southern Gulf. Although estimates of the consumption of cod by harp seals are low compared with consumption by grey seals if based on the limited diet data available for the southern Gulf, greater estimates are obtained assuming the high-cod diets seen at some times in some other areas (Hammill and Stenson 2002). Abundance trends were also roughly parallel between the harp and grey seal herds in the Gulf until the mid-1990s when harp seal abundance stabilized but grey seal abundance appeared to decrease (Hammill and Stenson 2002). Thus, the conclusion that seal predation on southern Gulf cod likely increased from the late 1970s to the mid-1990s remains valid consid-

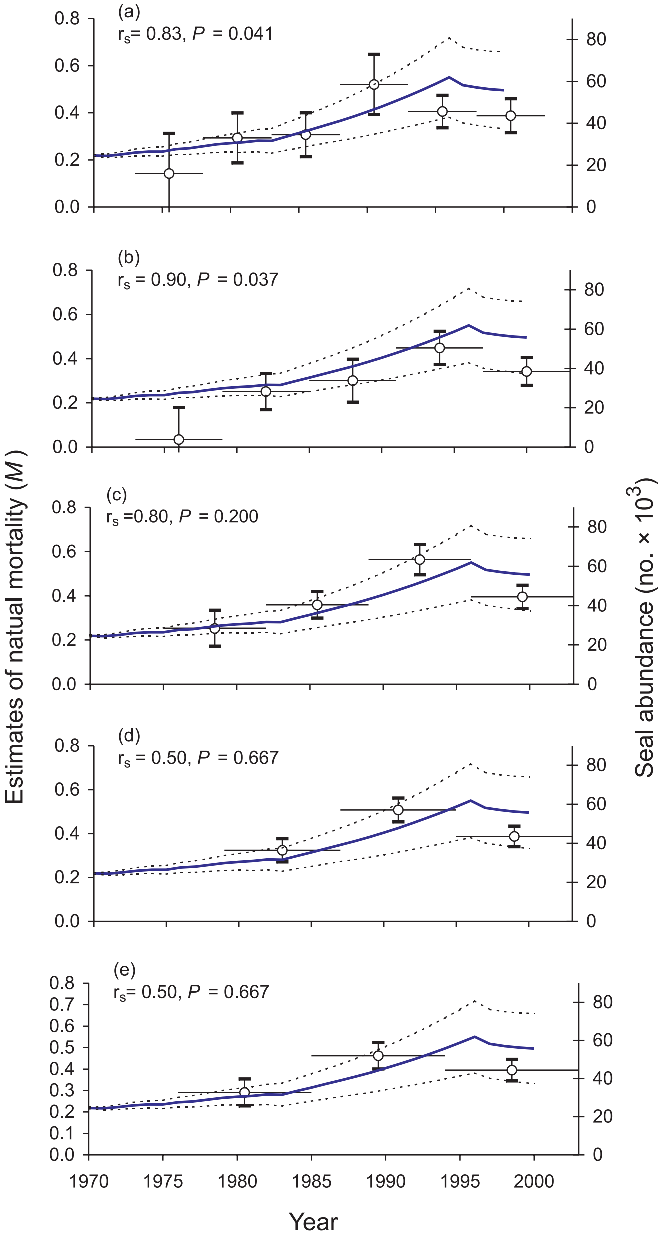


Fig. 4. Estimated *M* for periods of (*a*) 5, (*b*) 6, (*c*) 7, (*d*) 8, and (*e*) 9 years (circles with horizontal lines spanning the period covered) from the population analyses of southern Gulf of St. Lawrence Atlantic cod (*Gadus morhua*) and trends in the grey seal (*Halichoerus grypus*) population (solid lines) with confidence interval (broken lines). Error bars for estimates of *M* and confidence intervals for grey seal population estimates are ±2 SE and r_s is Spearman's correlation coefficient calculated using the estimated *M* and the average seal abundance during each period.

ering potential predation by harp seals and Sable Island grey seals in addition to predation by the Gulf grey seal herd.

It is becoming increasingly recognized that *M* increased for many cod stocks in Atlantic Canada during the 1980s. Besides the estimates from Sinclair (2001) and this analysis, Fu et al. (2001) concluded that *M* might have been high recently for cod on the eastern Scotian Shelf. Shelton and Lilly (2000) noted that an increase in *M* in the late 1980s is now routinely incorporated in several stock assessments. We note that pinniped population abundance is also high in the areas occupied by several western Atlantic cod stocks where increases in *M* are assumed.

Our results are consistent with previous analyses (e.g., Sinclair and Murawski 1997) that suggested that an increase in *F* was the main reason for the decline of cod in the southern Gulf. However, our analyses also suggest that an increase in *M* played a role in the collapse of this stock and in its failure to recover. While diet data are limited and feeding studies suggest that grey seals mostly target small cod, observations of belly feeding by seals and the results of this study showing the parallel trends between grey seal abundance and estimated *M* for this cod population suggest that predation by seals on adult cod may be more important than previously thought.

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