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Assessing threats to species at risk using stage-structured state–space models: mortality trends in skate populations

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Abstract. Population models are needed to assess the threats to species at risk and to evaluate alternative management actions. Data to support modeling is limited for many species at risk, and commonly used approaches generally assume stationary vital rates, a questionable assumption given widespread ecosystem change. We describe a modeling approach that can be applied to time series of length composition data to estimate vital rates and test for changes in these rates. Our approach uses stage-structured population models fit within a Bayesian state–space model. This approach simultaneously allows for both process and observation uncertainty, and it facilitates incorporating prior information on population dynamics and on the monitoring process. We apply these models to populations of winter skate (*Leucoraja ocellata*) that have been designated as "endangered" or "threatened." These models indicate that natural mortality has decreased for juveniles and increased for adults in these populations. The declines observed in these populations had been attributed to unsustainable rates of bycatch in fisheries for other groundfishes; our analyses indicate that increased natural mortality of adults is also an important factor contributing to these declines. Adult natural mortality was positively related to grey seal (*Halichoerus grypus*) abundance, suggesting the hypothesis that increased adult mortality reflected increased predation by expanding grey seal herds. Population projections indicated that the threatened population would be expected to stabilize at a low level of abundance if all fishery removals were eliminated, but that the endangered population would likely continue to decline even in the absence of fishery removals. We note that time series of size distributions are available for most marine fish populations monitored by research surveys, and we suggest that a similar approach could be used to extract information from these time series in order to estimate mortality rates and changes in these rates.

Key words: Bayesian analysis; fishing mortality; Leucoraja ocellata; *natural mortality; recovery potential; species at risk; stage-structured population models; state–space models; winter skate.*

Introduction

Widespread and precipitous declines in marine fishes have occurred in recent decades (Hutchings 2000, Baum et al. 2003, Myers and Worm 2003, Hutchings and Reynolds 2004). While overexploitation is clearly the main cause of these declines, changes in population productivity have also occurred in some cases (e.g., Shelton et al. 2006), either due to fisheries-induced evolutionary changes in the composition of populations (e.g., Olsen et al. 2004, Swain et al. 2007) or due to changes in their ecosystems (e.g., Swain and Sinclair 2000, Chouinard et al. 2005, Myers et al. 2007).

In order to develop recovery plans for collapsed populations, it is necessary to evaluate the potential causes of decline and the predicted effects of different management actions on population trajectories. For well-studied populations, this can be done using population models that incorporate information on abundance, age structure, and vital rates (e.g., Chouinard et al. 2005). This task is more daunting for poorly studied species for which the information required to fit these models is lacking.

Relative abundance of marine fishes has been monitored by long-term annual surveys in many areas. While detailed information on age composition is usually collected for only a handful of the most important commercial species, information on length composition is typically collected for most or all fish species. In this paper, we describe a modeling approach for extracting information from these time series of length composition data to estimate vital rates and test for changes in these rates. This approach, suitable for many data-poor species, permits inferences on the causes of population declines and on future population abundance under different management scenarios.

Our approach uses stage-structured population models fit to time series of survey data on relative abundance

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at length. We use Bayesian state–space models, which consist of two coupled components, a process model and an observation model. The process model describes the unobservable stochastic processes governing the population's dynamics, while the observation model describes the relationship between the unobserved states and the data that are observed with error. The Bayesian approach facilitates the incorporation of prior information on process and observation model parameters for which the data are uninformative, and deals naturally with lognormal process variability and observation errors. Bayesian state–space or hidden process models have been advocated for their flexibility in modeling complex population dynamics with data containing complex structures of natural variability and observation error (Schnute 1994, Clark and Bjornstad 2004, Buckland et al. 2007). Our approach represents a specific case of this broader class of models. We illustrate this approach using a case study on winter skate (*Leucoraja ocellata*, Family Rajidae; see Plate 1), a data-poor species at risk in the southern Gulf of St. Lawrence and eastern Scotian Shelf regions of Atlantic Canada.

Case study: winter skate in the southern Gulf of St. Lawrence and on the eastern Scotian Shelf

Winter skate are endemic to the Northwest Atlantic, occurring from Cape Hatteras to the northern Gulf of St. Lawrence and southern Newfoundland, Canada. In May 2005, the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) designated winter skate in the southern Gulf of St. Lawrence (SGSL) as "endangered" and those on the eastern Scotian Shelf (ESS) as "threatened" (COSEWIC 2005). These designations were based on (1) the life history characteristics of this species that increase its vulnerability to exploitation, and (2) 98% and 90% declines, respectively, in the abundance of mature individuals since the early 1970s. COSEWIC considered unsustainable bycatch rates in fisheries for other groundfish species to be the probable cause of these declines.

We use stage-structured population models to evaluate the causes of these declines. We conclude that an increase in the natural mortality of adults appears to be an important cause of the declines. We then extend the population models to examine potential explanatory factors for the change in natural mortality. Finally, we use these models to project future population abundance under different management scenarios.

Life history and ecological characteristics

Most skates have life history characteristics, such as late age at maturity, that make them susceptible to overexploitation. Over most of their range, including the ESS, winter skate are no exception, with 50% maturity at a length of about 75 cm and an age of about 12 years (Simon et al. 2003, Sulikoswki et al. 2003, Frisk 2004, McPhie 2007).

Winter skate in the SGSL appear to be distinct from populations in the remainder of the species' range (McEachran and Martin 1977). Outside of the Gulf, winter skate are sympatric with a closely related species, the little skate *L. erinacea*. McEachran and Martin (1977) suggest that the differences between winter skate inside and outside of the Gulf reflect character displacement between little and winter skate in areas of sympatry. Length at maturity for SGSL winter skate is about 42 cm (J. M. Hanson, *personal communication*), similar to the length at maturity of little skate in other areas (43–46 cm; Frisk 2004). Age at maturity of little skate is estimated to be 6.5–7 yr (Frisk 2004). Because its maximum length and length at maturity are about the same as those of little skate, in the analyses presented here we assume that the life history characteristics of SGSL winter skate more closely resemble those of little skate than those of winter skate in other areas. Preliminary aging data for SGSL winter skate support this assumption (D. P. Swain, *unpublished data*).

Skates are oviparous, depositing a single egg in a horny capsule or purse. Average annual fecundity is reported to be 50 purses for winter skate (McPhie 2007, Parent et al. 2008) and 30 for little skate (Frisk et al. 2002). Gestation time within the purses is 18–22 months for winter skate and 6–9 months for little skate (Scott and Scott 1988, Sulikoswki et al. 2003). Estimates of predation rates on skate egg cases range from 14% to 42% and average 24% for all studies to date (Lucifora and Garcia 2004). Length at hatching is 11–15 cm for winter skate and 9.5–10 cm for little skate (Scott and Scott 1988, Simon et al. 2003, Frisk 2004). After hatching, winter and little skate are eaten by many predators, such as sharks, other rays, and grey seals (Scott and Scott 1988).

Winter skate occur in warm shallow waters in inshore areas of the SGSL in summer and fall (Appendix A), and move offshore in winter. Smaller skates tend to occupy somewhat warmer and shallower water in the SGSL based on survey catches in September (Swain et al. 2006). Winter skate are found predominantly on the offshore banks on the ESS (Appendix A), moving up onto the banks in summer and into deeper water along the slopes of the banks in winter.

METHODS

Data sources

Data on relative abundance at length are from bottom-trawl surveys conducted each September since 1971 in the SGSL and each July since 1970 on the ESS. Surveys followed a stratified random design with stratification based on depth and geographic area. The stratified mean catch per 1.75-nm tow was used as an index of relative abundance. See Swain et al. (2006) and Appendix B for details.

In the SGSL, winter skate are caught in fisheries for other groundfish but are discarded at sea. Benoît (2006) estimated discarded bycatch (kg) of winter skate in groundfish and shrimp fisheries in the SGSL based on data collected by at-sea observers. These estimates of bycatch weight were converted to numbers discarded at length based on length composition of the survey population and selectivity of the commercial gear (details in Swain et al. 2006).

Fishery removals of winter skate on the ESS have been a combination of landed catch from a directed fishery (conducted from 1994 to 2004), discarded bycatch in domestic fisheries for other groundfish, and landed bycatch in foreign fisheries directing for other species. Reported landings, estimated bycatch, and the estimated size composition of landings and discarded bycatch are reported by Swain et al. (2006).

Population model

Because age-disaggregated data were not available for these populations, we used stage-structured population models. The SGSL model consisted of a juvenile stage comprised of skates 21–41 cm in total length (TL), and an adult stage comprised of skates 42 cm or longer. The ESS model included an adult stage (TL $\geq$ 75 cm) and two juvenile stages, one vulnerable to the directed skate fishery (60–74 cm TL) and one not yet vulnerable to the fishery (36–59 cm TL). Skates smaller than 36 cm TL were excluded from the ESS model due to difficulties in distinguishing between winter and little skates at these small sizes. Two types of models were examined. One focused on estimating total mortality rates (*Z*-models). The second type explicitly incorporated fishery removals and estimated natural mortality rates (*M*-models). Following Meyer and Millar (1999), we assumed multiplicative lognormal error structure. In the ESS *Z*-models, transitions from year $t - 1$ to year t were modeled as follows:

$$N_{1,t} = \left[N_{1,t-1}(1-\theta_1) + \frac{1}{2}(rN_{3,t-a})\right]e^{-Z_{1,t}}e^{\eta_{1,t}} \quad (1)$$

$$N_{2,t} = [N_{2,t-1}(1-\theta_2) + N_{1,t-1}\theta_1]e^{-Z_{2,t}}e^{\eta_{2,t}} \quad (2)$$

$$N_{3,t} = (N_{3,t-1} + N_{2,t-1}\theta_2)e^{-Z_{3,t}}e^{\eta_{3,t}} \quad (3)$$

where $N_{i,t}$ ($i = 1, 2, 3$) is abundance in year t for the ith life stage, θ_i is the transition probability to the next stage, a is the time between laying of egg cases and recruitment to juvenile stage 1 (5 yr), $Z_{i,t}$ is the stage-specific instantaneous rate of total mortality in year t, and r is the recruitment rate (i.e., annual fecundity per female discounted by egg case mortality and mortality between hatching and recruitment). A sex ratio of 1:1 was assumed to compute recruit production. The probability of transition directly from the first juvenile stage to the adult stage in one year was assumed to be zero based on plausible growth rates for winter skate. The $\eta_{1,t}$, $\eta_{2,t}$, $\eta_{3,t}$ are independent normal random variables with mean zero and variance σ_i^2, representing process stochasticity in each of the three stages. The SGSL model has the same form except that transition was directly from the first juvenile stage to the adult stage and a was set to two years, reflecting a shorter incubation period and earlier age of recruitment to the juvenile stage (Appendix C).

Transitions were the same in *M*-models except that fishing and natural mortality were modeled separately. For example, Eq. 3 was modified as follows:

$$N_{3,t} = [(N_{3,t-1} + N_{2,t-1}\theta_2)(1 - E_{3,t})]e^{-M_{3,t}}e^{\eta_{3,t}} \quad (4)$$

where $M_{3,t}$ and $E_{3,t}$ are the rates of natural mortality and exploitation for the adult population in year t, $E_{3,t} = C_{3,t}/(N_{3,t-1} + N_{2,t-1}\theta_2)$, where adult catch $C_{3,t}$ is the sum of discarded adults $D_{3,t}$ multiplied by a discard mortality rate α and landed adults $L_{3,t}$; $C_{3,t} = \alpha D_{3,t} + L_{3,t}$. For simplicity we assumed that α is equal for juveniles and adults.

For all models we assumed that recruitment and transition between stages occurred prior to mortality events. For the *M*-models we also assumed that fishing mortality occurred prior to natural mortality.

Observation model

The true abundance of each life stage $N_{i,t}$ is not observed directly; rather, survey catch rates provide observations of relative abundance $y_{i,t}$ with some error. Survey catch rates can be related to $N_{i,t}$ with the following observation model:

$$y_{i,t} = q_i N_{i,t} e^{\varepsilon_{i,t}} \quad (5)$$

where q_i is the catchability coefficient of stage i that scales relative abundance to $N_{i,t}$ ($i = 1, 2, 3$), and $\varepsilon_{i,t}$ are independent normal random variables with mean zero and variance τ_i^2, representing observation error in the abundance index for stage i.

In the *Z*-models, the survey catch rates were adjusted for size selectivity using the research-trawl selectivity curve estimated by Harley and Myers (2001) for flatfish. Small and large individuals were adjusted to the same relative catchability, but not to 100% catchability, by setting the maximum catchability (γ' in Harley and Myers [2001]) to one. In models with fishery removals, we scaled the indices to absolute abundance by (1) fully adjusting for catchability, (2) adjusting for availability, and (3) expanding from swept area to survey area (Appendix B).

Alternative models

For both the *Z*- and *M*-models we fit a number of alternatives with respect to the mortality parameters $Z_{i,t}$ or $M_{i,t}$. These parameters were either (1) constrained to be constant, (2) allowed to vary by decade (i.e., 1970s, 1980s, and 1990–2004), (3) allowed to follow a random walk, (4) assumed to follow a time trend, or (5) in the *M*-models, assumed to be a function of a covariate such as predator abundance or environmental conditions. In the time trend models, mortality rate was assumed to be a linear or quadratic function of time in years. Alternative models were compared using the deviance information criterion (DIC; Spiegelhalter et al. 2002). The DIC statistic is a Bayesian analogue of AIC for model selection.

Covariate models were examined for M_i only. Potential explanatory factors examined were the abundances of grey seals (*Halichoerus grypus*) and large cod or indices of water temperature conditions (Swain et al. 2006). Prior to stock collapses in the early 1990s, cod was the dominant demersal fish (in terms of biomass) in the SGSL, and was also among the most important demersal fishes on the ESS. Piscivory by cod increases with size, with fish representing an important component of the diet of large ($\geq$60 cm) cod (Hanson and Chouinard 2002). We used the relative abundance of cod $\geq$60 cm in length (based on mean catch rates in the annual trawl surveys) as an index of predation by cod on small fishes in both ecosystems. Grey seals (*Halichoerus grypus*) are also important piscivores in both systems and estimated abundances of grey seals in the Gulf and Sable Island (ESS) herds were used as indices of piscivory by grey seals in each ecosystem. Time series of total population abundance were taken from Hammill (2005) for the Gulf herd and provided by R. K. Mohn (Department of Fisheries and Oceans, Dartmouth, Nova Scotia) for the Sable Island herd. During the summer feeding season, winter skate occur in the cold intermediate layer (CIL) on the ESS and in the shallower warm water layer in the SGSL. A CIL temperature index (mean temperature at 100 m on Misaine Bank) was used as a covariate of M_i in models for the ESS, whereas mean temperature in shallow inshore waters was used as a covariate of M_i in models for the SGSL. All covariates were standardized by subtracting their minimum and dividing by their standard deviation.

Bayesian analysis

We used a Bayesian approach to parameter estimation, placing informative priors on a number of model parameters (Table 1 and Appendix C) for which little information was likely to be available in the relative abundance at length data. In particular, we made use of previously published data on annual fecundity (Frisk et al. 2002, Parent et al. 2008), growth rate (Sulikowski et al. 2003, Frisk 2004), mortality prior to recruitment (egg case and early juvenile stages; Frisk et al. 2002, Lucifora and Garcia 2004), and discard mortality (Benoît 2006; see Appendix C for details). Because we adjusted the relative abundances for size selectivity prior to state–space modeling we placed highly informative priors on the catchability q of each life stage. In most cases, we assumed that catchability with the adjusted catch rates was 1.0 but allowed some variation about this value. The exception was the q for juveniles in the SGSL Z-model; the prior distribution for this q had a mean of 0.7 (95% CI of 0.52–0.94) to account for the lower availability of juveniles than adults to the survey of the SGSL. Priors for initial population sizes were based on the average survey catch rates in the early to mid 1970s and were highly informative. Uniform priors were placed on all other model parameters (Table 1, Appendix C). Lower limits for the priors for observation error were based on the coefficient of variation of the survey data. Plots comparing priors and posteriors for selected models are shown in Appendix E.

We used the freely available software WinBUGS (Version 1.4.1; Lunn et al. 2000) to implement the state–space models. The software uses Gibbs sampling (Gelman et al. 2005), a Markov Chain Monte Carlo (MCMC) approach, to estimate the joint posterior distribution of the model parameters. A total of 175 000 samples was generated in each of two chains, the first 100 000 were discarded as a "burn-in," and every 30th sample thereafter was retained to reduce autocorrelation, yielding 5000 samples from the joint posterior. We selected contrasting values within the range specified by each of the prior distributions to initialize the two chains; these values are given in Appendix F. Convergence was assessed by examining plots of Brooks, Gelman, and Rubin convergence statistics and by comparing posterior density plots for the first, middle, and last third of the saved iterations for each chain. Examples are shown in Appendix G. Example model code and data for both winter skate populations are provided in Appendix D and in the Supplement.

Sensitivity analysis

We expected the posterior distributions for mortality parameters to be influenced by the ratio of juveniles to adults in the data and by the prior distribution used for θ. The ratio of juveniles to adults in the SGSL data depends on whether the abundance indices are adjusted to day or night catchability since the diel difference in catchability is strongly length dependent. Adjustment of the SGSL data for the diel difference in catchability was required due to a change in survey procedures (see Appendix B). We compared posterior distributions for mortality parameters between day- and night-adjusted survey catch rates for the SGSL population. We also examined the effect of the prior distribution for θ on these parameters for the SGSL population. Finally, we examined the sensitivity of patterns in natural mortality to the estimated scaling of population abundance vs. fishery catch. If fishery catch is underestimated or population abundance overestimated, then the importance of natural mortality to population trends will be overestimated. We examined the sensitivity of our results to the relative scaling of fishery catch and population abundance by comparing results using either the median or the 95th percentile of estimated catch as the input to SGSL M-models.

We also examined whether apparent changes in mortality could instead reflect changes in juvenile growth. We simulated changes in juvenile growth by allowing or assuming decadal variation in θ in SGSL models. In model $\Delta G1$, Z was assumed to be constant over time and vague uniform priors were used for both

TABLE 1. Priors on parameters for the *Z*- and *M*-models for winter skate (*Leucoraja ocellata*) in the southern Gulf of St. Lawrence (SGSL) and on the eastern Scotian Shelf (ESS).

Parameter	SGSL		ESS	
	Z	*M*	*Z*	*M*
Mortality parameters				
1) Constant mortality or decadal variation in mortality				
Juveniles	uniform(0,5)		uniform(0,3)	
Adults	uniform(0,3)		uniform(0,3)	
2) Random walk				
Juvenile, Z_0	uniform(0,5)		uniform(0,5)	
Adult Z_0	uniform(0,3)		uniform(0,5)	
Error (SD)	uniform(0,2)		uniform(0,2)	
3) Time trend or covariate models				
Intercepts	uniform(0,5)		uniform(0,5)	
Slopes	uniform(−1,1)		uniform(−1,1)	
Other parameters				
r	lognormal(2.014903, 7.11111) *I*(0.01,1000)		lognormal(1.178655, 4) *I*(0.01,1000)	
θ_1	beta(20,80) *I*(0.15,0.25)		beta(20,80)	
θ_2			beta(25,75)	
α	beta(30,70)		beta(30,70)	
τ_1	uniform(0.50,2)		uniform(0.497,2)	
τ_2	uniform(0.36,1)		uniform(0.586,2)	
τ_3			uniform(0.513,2)	
σ_i	uniform(0,2)		uniform(0,5)	
q_1	lognormal(−0.357,44.44)	lognormal(0,100)	lognormal(0,100)	lognormal(0,100)
q_2, q_3	lognormal(0,100)	lognormal(0,100)	lognormal(0,100)	lognormal(0,100)
$N_{1,-1}$	lognormal(−1.3863,6.25)	lognormal(1.0986,100)	lognormal(0,6.25)	lognormal(2.56495,100)
$N_{2,-1}$	lognormal(−0.9163,16)	lognormal(1.6094,100)	lognormal(−1.204,6.25)	lognormal(1.30833,25)
$N_{2,-2}$	lognormal(−0.9163,16)	lognormal(1.6094,100)		
$N_{3,i}$ I (−5,−1)			lognormal(1.2528,11.11)	lognormal(3.82864,400)

Notes: Abundance parameters ($N_{i,j}$) are on a relative scale (fish/tow) in *Z*-models and on an absolute scale (10^6, SGSL; 10^5, ESS) in *M*-models. *Z*-models estimate total mortality rates whereas *M*-models incorporate fishery removals and estimate natural mortality rates. Models were also run using zero-truncated normal priors instead of lognormal priors and produced similar results and the same conclusions as the models described here. The second parameter of the normal distribution is given as precision ($1/\sigma^2$). The notation $I(x, y)$ indicates that distributions are truncated at x and y so that values must be greater than x and less than y. Other parameters are: r, the recruitment rate; θ_i, the transition probability to stage $i + 1$; α, the discard mortality rate; τ_i, the standard deviation (SD) for observation error; σ_i, the SD for process error; q_i, the catchability coefficient for stage i; $N_{i,-j}$, the abundance of stage i in year $-j$ (i.e., j years before the start of the time series of abundance indices). For further details see the *Methods*: *Population model* and *Observation model*.

Z and θ. Priors covered the range 0–5 for juvenile Z, 0–3 for adult Z, and 0.1–0.35 for θ in each decade. We considered this range for θ to exceed the range of plausible growth rates, representing growth from 21 to 41 cm in three ($\theta = 0.33$) to 10 ($\theta = 0.1$) years. In models $\Delta G2$ and $\Delta G3$, both Z and θ were allowed to vary on a decadal scale. In model $\Delta G3$, vague uniform priors were used for θ as in model $\Delta G1$. In model $\Delta G2$, decadal variation in θ was forced by using different informative priors for the θ in different decades: beta(30, 70) I(0.25, 0.35) for the 1970s, and beta(15, 85) I(0.1, 0.2) for the 1980s and 1990+. The $I(x, y)$ denotes truncation such that values must be greater than x and less than y.

RESULTS

Trends in abundance and fishery removals

In the southern Gulf of St. Lawrence (SGSL), abundance of mature (≥42 cm) winter skate declined in the 1980s and has been very low since the mid 1990s (Fig. 1a). Abundance of juvenile skates (21–41 cm) was low in the early 1970s, increased to relatively high levels in the mid to late 1980s, and then declined to a low level in recent years. No landings of winter skate have been reported from the SGSL. Estimates of discarded bycatch were highest in the 1970s and have been at a very low level since the early 1990s (Fig. 1b). Low bycatch since the early 1990s reflects low skate abundance as well as low fishing effort following the collapse of cod and other groundfish stocks in the SGSL.

On the eastern Scotian Shelf (ESS), estimated abundance of mature (≥75 cm) winter skate was highest in the 1970s and has been low since the mid 1990s (Fig. 2a). Estimated abundance of juvenile winter skate on the ESS tended to be low in the early to mid 1970s and relatively high from the late 1970s to the mid 1990s. Landings of winter skate on the ESS tended to be highest in the early to mid 1970s and the early to mid 1990s and have been relatively low in recent years (Fig.

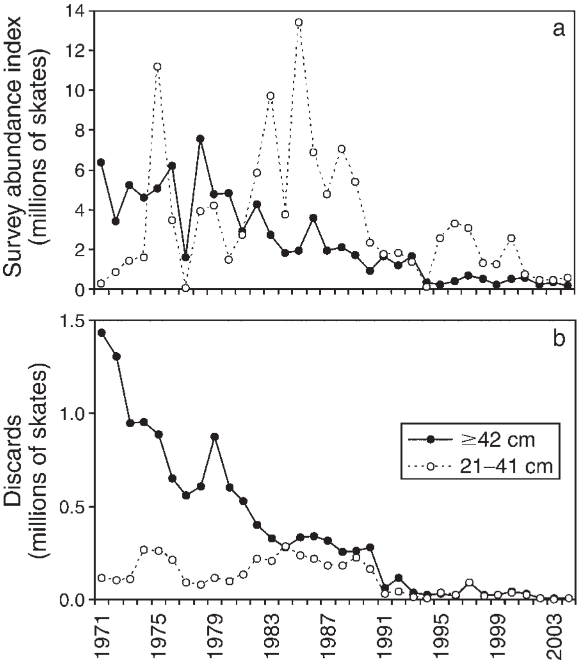

FIG. 1. (a) Survey abundance indices and (b) estimated discarded catch for two length classes of winter skate (*Leucoraja ocellata*) in the southern Gulf of St. Lawrence from 1971 to 2004.

2b). The high landings before 1977 were by foreign fleets that were excluded from most of the ESS in 1977; those in the mid 1990s were by a directed skate fishery that opened in 1994. Estimates of discarded catch were relatively high from the late 1970s to the early 1990s and have been very low since the mid 1990s (Fig. 2c). This variation in discarded catch reflects variation in effort by domestic fleets directing for other groundfishes.

Trends in total mortality

The constant-mortality model yielded median estimates of 1.4 and 0.35 for Z of juvenile and adult winter skate in the SGSL, respectively. However, this model did not fit the abundance trends well, tending to overestimate juvenile abundance in the early 1970s, underestimate juvenile abundance throughout the 1980s and 1990s, and underestimate adult abundance in the 1970s (Fig. 3a, b). Fit to the observed abundance trends was substantially improved by allowing for decadal variation in Z (Fig. 3c, d). Estimated adult Z increased from the 1970s to the 1980s, whereas estimated juvenile Z decreased over the same period (Fig. 4a, b). Models in which Z was assumed to follow a continuous time trend or a random walk over time were also a substantial improvement over the model with constant Z, fitting the abundance data about as well as the model with decadal variation in Z. Deviance information criterion (DIC) was −135.5 for the constant-mortality model, and similar (−166.1 to −160.9) for all models that allowed temporal variation in Z (Table 2). Based on DIC, the best model was the model with a linear trend in adult Z and a quadratic trend in juvenile Z (DIC = −166.1). Changes over time in Z estimated by the random walk and time trend models (Appendix H) were consistent with those estimated by the model with decadal variation in Z.

Assuming constant mortality over the period from 1970 to 2004, posterior medians for Z on the ESS were 0.49 for the first juvenile stage, 0.41 for the second stage, and 0.22 for the adult stage. A model allowing decadal variation in Z indicated temporal patterns similar to those estimated for skate in the SGSL, with Z declining from the 1970s to the 1980s for the small juvenile size class, roughly constant over time for larger juveniles, and increasing over time for adults (Fig. 5a–c). However, evidence for changes in Z were not as strong for ESS skate, with broad overlap between time periods in the posterior distributions for Z. DIC was similar between the models assuming constant Z or decadal

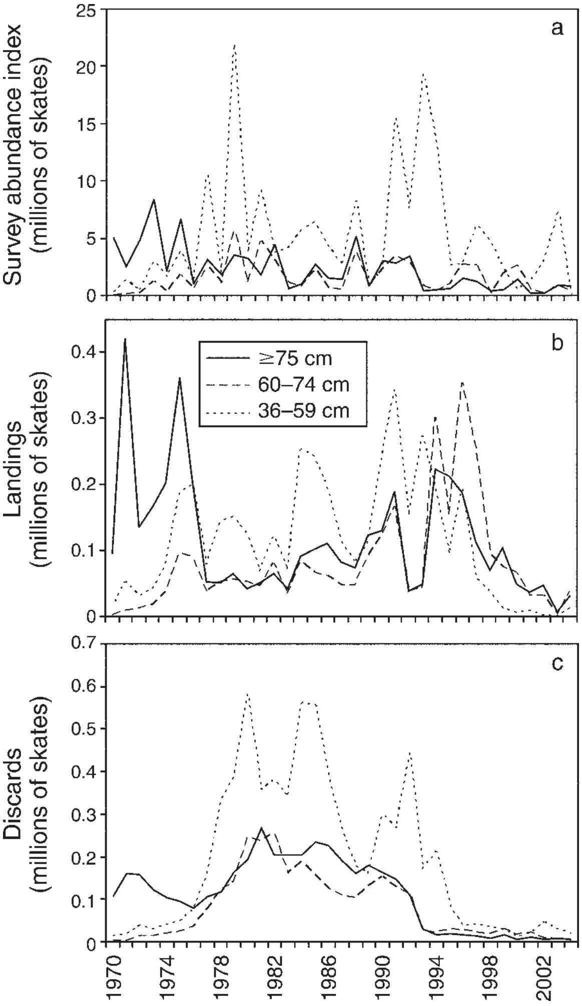

FIG. 2. (a) Survey abundance indices and (b, c) estimates of landed and discarded catch, respectively, for three length classes of winter skate on the eastern Scotian Shelf.

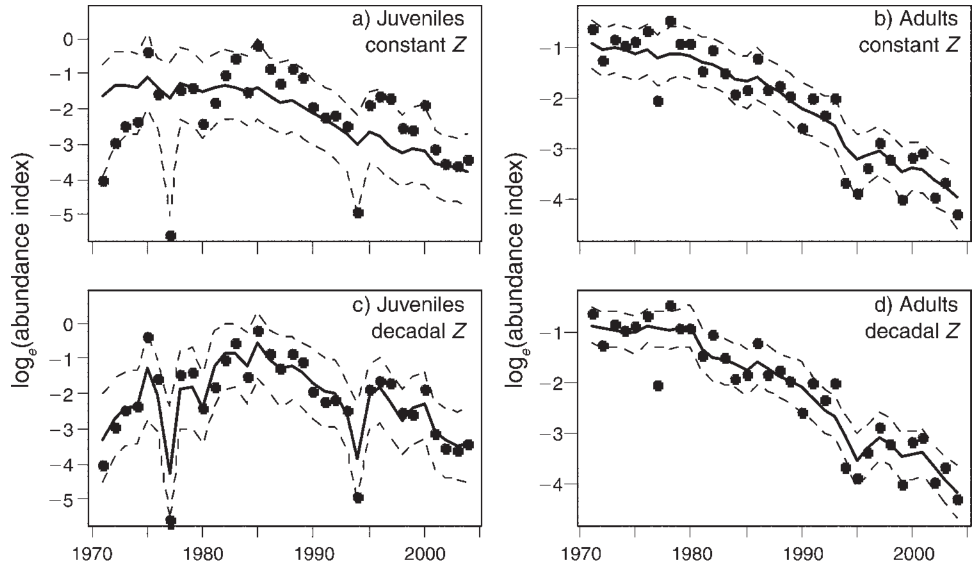

FIG. 3. Abundance trends ($\log_e$-transformed number of fish per tow) for juvenile (21–41 cm total length) and adult (≥42 cm total length) winter skate in the southern Gulf of St. Lawrence. Circles show the observed indices, and lines the median (solid) and 95% credible limits (dashed) of the posterior distribution of the predicted indices for models assuming constant mortality rates (a, b) or allowing decadal variation in mortality (c, d).

variation in Z, but somewhat smaller for models assuming a random walk or trends over time in Z (Table 2). These latter models indicated changes over time in Z similar to those indicated by the decadal model (Appendix H).

Trends in exploitation rate and natural mortality

Results described in this section are restricted to those for models assuming decadal variation in natural mortality (M). Models that assumed temporal trends in M (like those examined for Z) led to similar conclusions and are not reported here (except for their DIC values in Table 2).

Estimated exploitation rate was very low throughout the 1970–2004 period for juvenile winter skate in the SGSL (Fig. 4c). For adults in the SGSL, exploitation rate was relatively high in the early 1970s, but declined throughout the 1970s and 1980s, and has been very low since the early 1990s (Fig. 4d). The trends in exploitation rate and total mortality were in opposite directions for adults, indicating that the increase in adult mortality after the 1970s appeared to be due to an increase in

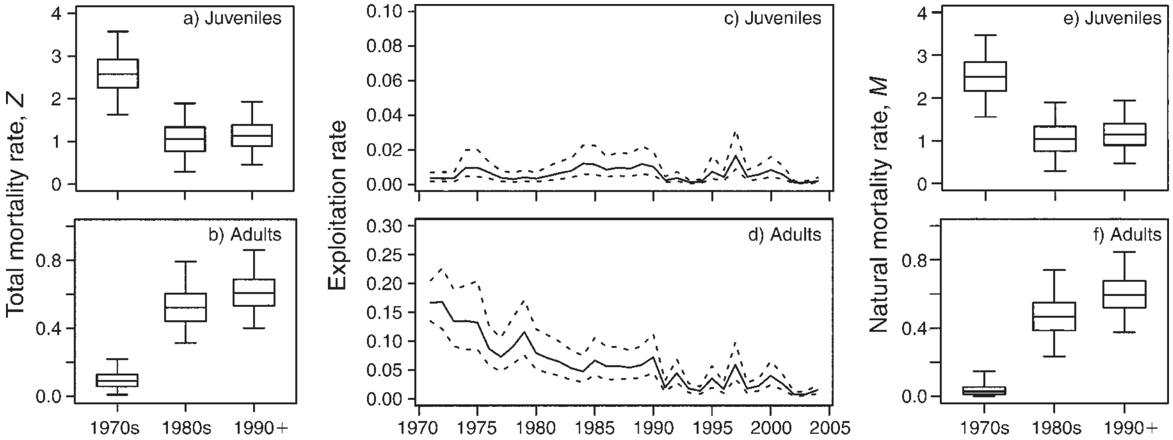

FIG. 4. Estimated trends in the rates of total mortality (Z), exploitation, and natural mortality (M) of juvenile and adult winter skate in the southern Gulf of St. Lawrence, based on models allowing decadal variation in Z (a, b) or M (c–f). Exploitation rate is the removal by fishing (landed catch and discard mortalities) as a proportion of beginning-of-year abundance (i.e., abundance after recruitment and transition between stages, but before losses due to fishing and natural mortality). Box plots show the median, interquartile range, and 95% credible limits of the posterior distributions of Z (a, b) and M (e, f). Solid lines show the median, and dashed lines show the 95% credible limits for the posterior distribution of exploitation rate (c, d).

TABLE 2. Values of the deviance information criterion (DIC) and effective number of parameters (pD) of population models for winter skate in the southern Gulf of St. Lawrence (SGSL) and on the eastern Scotian Shelf (ESS).

Model	DIC	pD
1) SGSL Z-model		
Constant Z	−135.470	12.723
Decadal variation	−164.949	19.534
Random walk	−163.297	19.681
Time trend QL†	−166.095	18.213
Time trend QQ	−164.625	19.801
Time trend LL	−164.814	15.553
Time trend LQ	−160.926	15.966
2) SGSL M-model		
Constant M	227.253	14.559
Decadal variation	197.420	20.163
Time trend QL	197.356	21.650
3) SGSL M covariate models (juvenile covariate, adult covariate)‡		
Time (Q), seals	204.834	20.823
Seals, seals	214.526	14.019
Cod, seals	211.813	15.809
Cod and seals, seals	217.011	14.295
Temperature, temperature	207.790	20.739
Cod and temperature, seals and temperature	210.116	19.760
4) ESS Z-models		
Constant Z	340.072	20.571
Decadal variation	341.585	22.225
Random walk	336.940	22.487
Time trend QCL§	331.885	19.086
5) ESS M-models		
Constant M	880.523	20.899
Decadal variation	881.558	21.794
Time trend QCL	873.123	19.670
6) ESS M covariate models (juvenile stage 1, adults)¶		
Time (Q), seals	872.780	19.358
Seals, seals	881.043	19.691
Cod, seals	879.946	19.723
Temperature, temperature	881.113	22.624

Note: Models estimate either total (Z) or natural mortality rates (M).

† Quadratic (Q) time trend for juveniles, linear (L) trend for adults.

‡ Covariate effects are assumed to be linear except for time (quadratic).

§ Quadratic time trend for juvenile stage 1, constant (C) Z for juvenile stage 2, and linear time trend for adults.

¶ M is assumed to be a linear function of covariates, except for quadratic time trends (denoted by Q). M of juvenile stage 2 is assumed to be constant.

natural mortality. For juveniles, decadal variation in estimated M was very similar to the variation in Z, reflecting their very low exploitation rate (Fig. 4a, c, e). For adults, the trend in estimated M was even stronger than the trend in Z, reflecting the opposing directions of trends in exploitation rate and M (Fig. 4b, d, f).

Estimated exploitation of all length classes of winter skate on the ESS was low to moderate throughout the 1970s and 1980s (Fig. 5d–f). For all length classes, estimated exploitation rate declined in the early 1990s, when fishing effort in groundfisheries decreased sharply. Exploitation of larger skates (60+ cm) increased with the start of the directed skate fishery in 1994, but declined in the late 1990s as catches in this fishery were reduced. The estimated exploitation rate has been very low in recent years for all length classes. Estimated trends in M (Fig. 5g–i) were similar to the trends in Z.

Potential causal factors

Both the SGSL and ESS ecosystems have undergone dramatic changes over the past 30 years (Choi et al. 2005, Benoît and Swain 2008). We examined whether changes in skate mortality might be related to changes in environmental conditions or the abundance of potential predators. Grey seal abundance has increased dramatically in both ecosystems over the past 30 years (Fig. 6a). The abundance of large (piscivorous) cod declined dramatically in both ecosystems from the mid 1980s to the early 1990s (Fig. 6b). Bottom temperatures during summer in the shallow waters occupied by winter skate in the SGSL have shown an increasing trend over the study period (Fig. 6c). Water temperatures at the mid depths occupied by winter skate on the ESS tended to be relatively cold from the late 1980s to the mid 1990s (Fig. 6d).

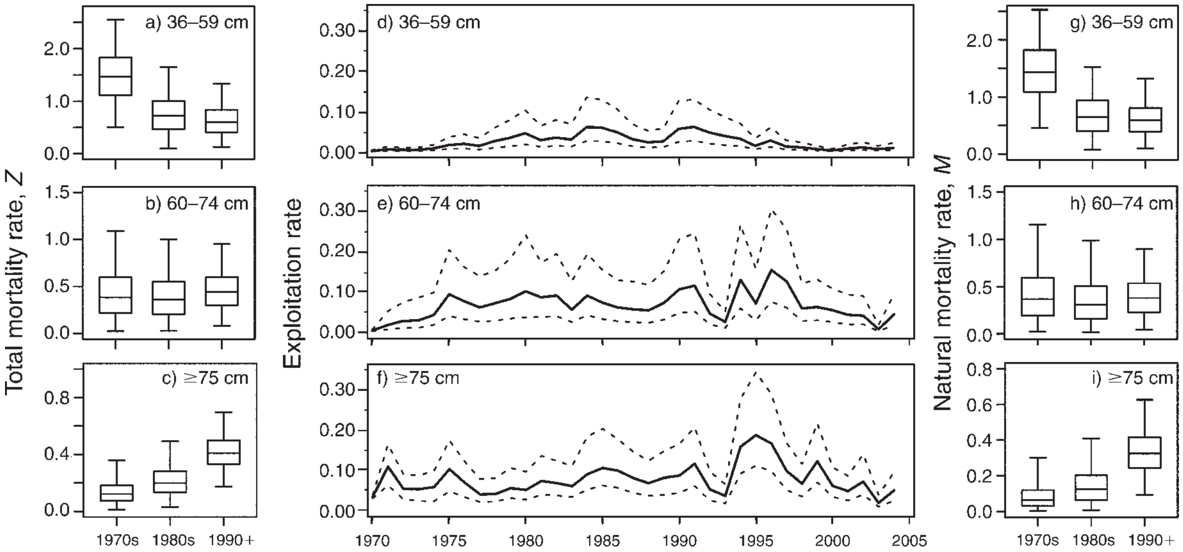

FIG. 5. Estimated trends in the rates of total mortality (Z), exploitation, and natural mortality (M) of three length classes of winter skate on the eastern Scotian Shelf, based on models allowing decadal variation in Z (a–c) or M (d–i). Box plots show the median, interquartile range, and 95% credible limits of the posterior distributions of Z (a–c) and M (g–i). Solid lines show the median, and dashed lines show the 95% credible limits for the posterior distribution of exploitation rate (d–f).

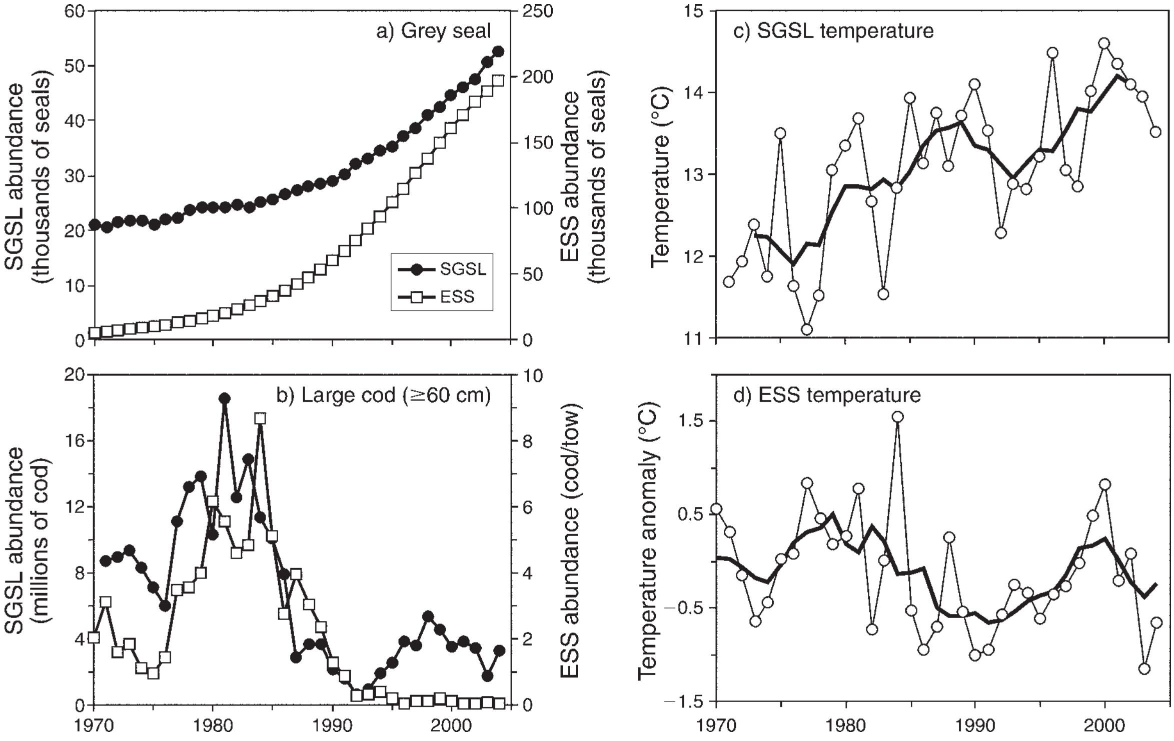

FIG. 6. Indices of ecosystem change in the southern Gulf of St. Lawrence (SGSL) and on the eastern Scotian Shelf (ESS): (a) grey seal abundance, (b) abundance of large cod (≥60 cm in length), (c) a bottom temperature index for inshore areas of the SGSL, (d) temperature at 100 m on Misaine Bank on the ESS. The index in panel (d) is the anomaly from the long-term (1971–2000) average. Heavy lines in panels (c) and (d) are five-year running means. In panel (b), the SGSL data are survey catch rates scaled up from the area swept by a tow to the survey area.

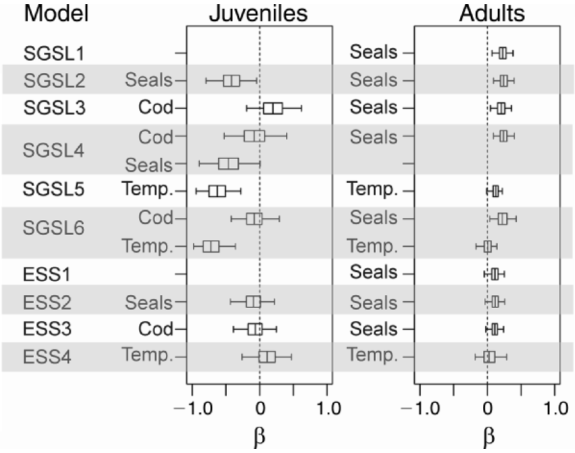

FIG. 7. Posterior distributions of slope parameters for covariates of natural mortality (*M*) of juvenile or adult skates in population models for the SGSL and the ESS. In ESS models, *M* for the first juvenile stage was a function of the covariate, while *M* for the second stage was assumed to be constant over time, based on the models with decadal variation in *M*. In models SGSL1 and ESS1, *M* for the (first) juvenile stage was assumed to be a quadratic function of time in years since 1970 or 1969, respectively. Box plots are as described in the Fig. 4 legend.

We examined the hypotheses that (1) trends in adult *M* reflect changes in predation by seals, (2) trends in juvenile *M* reflect changes in predation by seals and/or cod, and (3) trends in juvenile and/or adult *M* reflect changes in environmental conditions. A positive relationship between *M* and predator abundance was expected for direct effects of predation. No particular direction was expected a priori for relationships between *M* and environmental conditions.

In the SGSL, adult *M* showed a positive relationship with seal abundance regardless of the modeling approach taken for juvenile *M* (Fig. 7). In contrast, juvenile *M* was not related to indices of predator abundance in the expected positive direction, except in Model 3, in which it was modeled as a function of large cod abundance (Fig. 7). However, the relationship between juvenile *M* and cod abundance was weak, with the posterior for the slope parameter overlapping zero. Natural mortality showed a negative relationship with bottom temperature for juveniles and a positive relationship for adults. Models that included both predator abundance and temperature as covariates of *M* indicated that the relationship with *M* was stronger for temperature in the case of juveniles but stronger for predator (seal) abundance in the case of adults. The best covariate model in terms of DIC was the model with juvenile *M* a quadratic function of time and adult *M* a covariate of seal abundance (Table 2).

No relationship was evident between predator abundance or temperature and *M* of the first juvenile stage in models for the ESS (Fig. 7). Adult *M* was positively related to seal abundance and unrelated to temperature on the ESS. Based on DIC, the best model for the ESS was the model with *M* of the first juvenile stage a quadratic function of time and adult *M* a covariate of seal abundance (Table 2).

Population projections

In order to assess recovery potential, abundance was projected from 2004 to 2014, assuming various levels of fishery removals. In order to avoid extrapolating observed mortality trends into the future, the model assuming decadal variation in *M* was used, assuming that *M* in 2005–2014 was the same as *M* in 1990–2004. Based on these projections, abundance of adults in the SGSL is expected to continue to decline even with no fishery removals, though bycatch at the 2002–2004 level (10 Mg) would have a negligible effect on the decline (Fig. 8a). However, bycatch at a slightly higher level (50 Mg, the average level in 1993–2001) is expected to accelerate the decline substantially, with extirpation expected in just over 10 years. The 95% credible limits around the projected trends in abundance are wide but do not include recovery (if recovery is defined as achieving the abundance level observed in the 1970s, or the mean or median abundance level in the 1971–2004 period).

Projections for the ESS are slightly more optimistic (Fig. 8b). Adult abundance is expected to stabilize at a low level in the absence of fishery removals. Removals at the 2002–2004 level (230 Mg landed and 70 Mg discarded) would be expected to result in a continued decline in abundance. However, uncertainty around projected abundance was great, with the 95% credible limits encompassing both recovery (e.g., a return to the average abundance level in the 1970s) and extirpation (assuming fishery removals at the 2002–2004 level).

Sensitivity analyses

The values estimated for mortality parameters depend on catchability adjustments (which affect the ratio of adults to juveniles) and on the prior on θ (Fig. 9a, b). Mortality is estimated to be slightly lower for juveniles and higher for adults using data adjusted to night- vs. daytime catchability. Estimates of juvenile mortality were unaffected by the prior on θ, but adult mortality was estimated to be somewhat higher when the prior on θ was centered on higher values. However, temporal patterns in mortality were similar regardless of the prior used for θ or the catchability adjustment applied to the data. Finally, the estimated temporal trends in natural mortality were insensitive to uncertainty in the level of abundance relative to fishery removals. Mortality trends were similar using the 50th and the 95th percentiles of estimated fishery removals (Fig. 9c, d).

Models with decadal variation in θ suggest that patterns in the SGSL data that we have attributed to changes in mortality cannot instead be attributed to changes in juvenile growth. In model $\Delta G1$ (Fig. 10a–e), mortality is assumed to be constant over time. In this

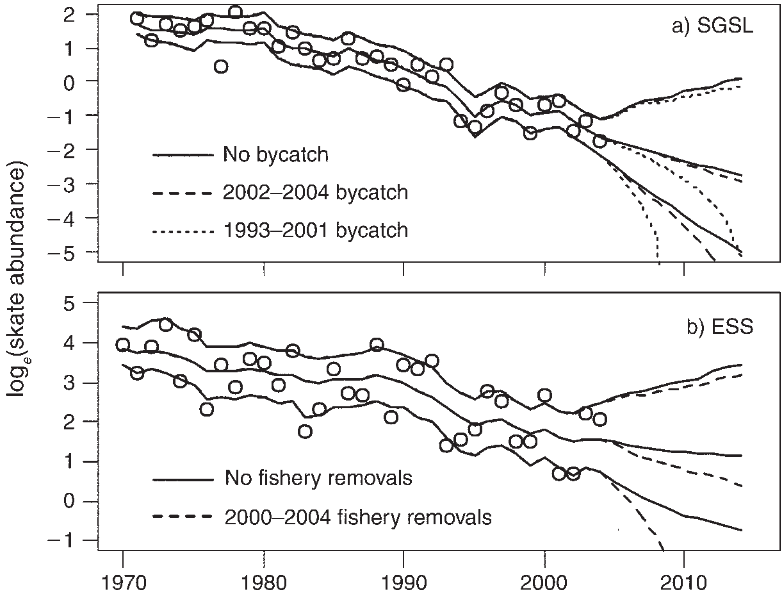

FIG. 8. Projected abundance of adult winter skate (a) in the SGSL and (b) on the ESS, assuming decadal variation in natural mortality (M) and various levels of fishery removals. M in 2005–2014 was assumed to be at the 1990–2004 level. Lines show the median of the posterior distribution of log$_e$-transformed abundance and the 95% credible limits. Abundance prior to log-transformation is (a) 10^6 or (b) 10^5 fish.

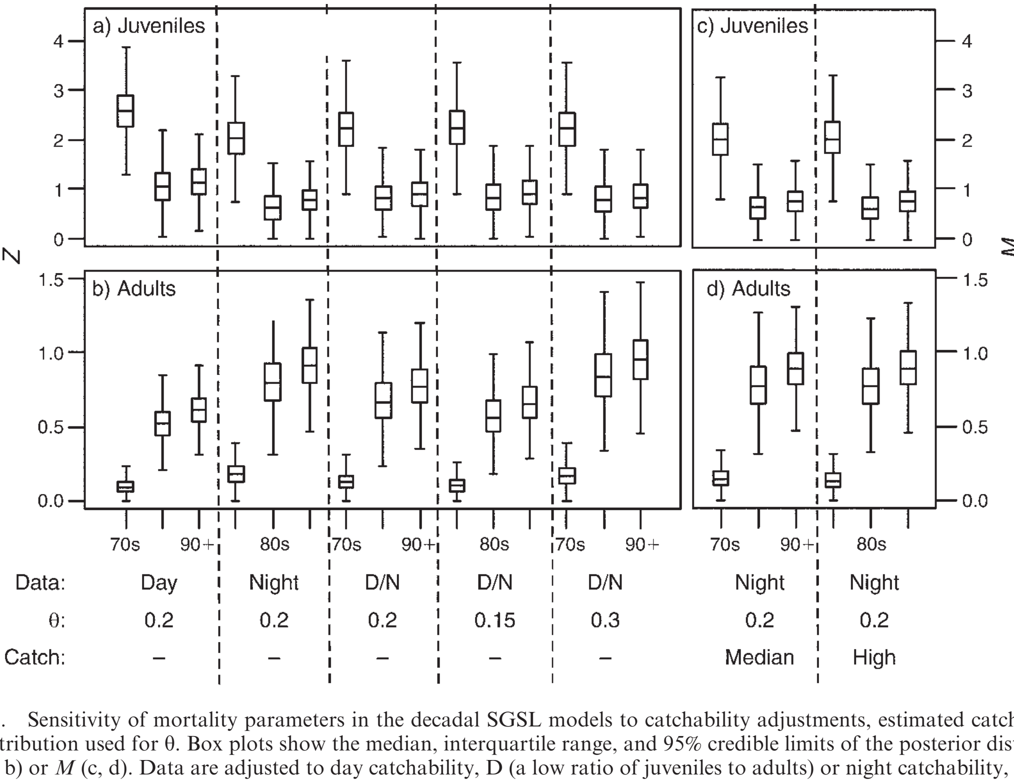

FIG. 9. Sensitivity of mortality parameters in the decadal SGSL models to catchability adjustments, estimated catch, and the prior distribution used for θ. Box plots show the median, interquartile range, and 95% credible limits of the posterior distributions for Z (a, b) or M (c, d). Data are adjusted to day catchability, D (a low ratio of juveniles to adults) or night catchability, N (a high ratio of juveniles to adults); in D/N runs, catch rates are adjusted to daytime catchability but the prior on juvenile catchability is adjusted to give an intermediate ratio of juveniles to adults. Priors on θ are: (1) 0.2: beta(20, 80)/(0.15, 0.25); (2) 0.15: beta(15, 85)/(0.1, 0.2); or (3) 0.3: beta(30, 70)/(0.25, 0.35). In panels (c) and (d), results are compared using the median or 95th percentile of estimated catch.

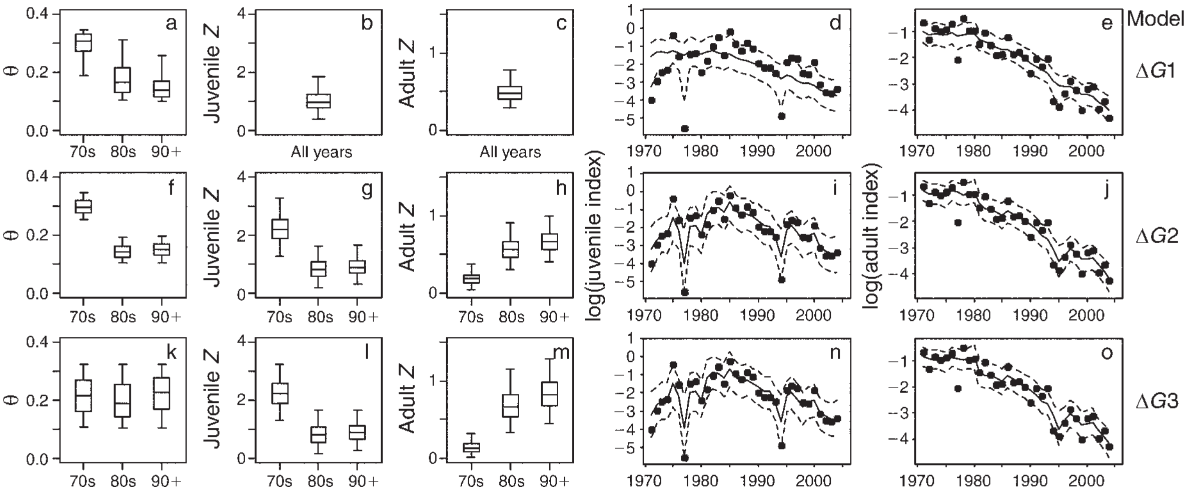

FIG. 10. Results for SGSL models simulating decadal variation in juvenile growth: Δ$G1$, Z assumed to be constant, decadal variation allowed in θ with vague uniform priors; Δ$G2$, decadal variation allowed in Z with vague uniform priors, decadal variation forced in θ by informative priors; Δ$G3$, decadal variation allowed in both Z and θ with vague uniform priors. See *Methods: Sensitivity analysis* for further details. Box plots show the median, interquartile range, and 95% credible limits of the posterior distributions for θ or Z. Circles show the log of the observed abundance indices, and solid and dashed lines show the median and 95% credible limits, respectively, of the predicted log indices.

model, the posterior distribution of θ is shifted toward the upper limit of the prior in the 1970s and the lower limit in later years (Fig. 10a). This corresponds to very rapid juvenile growth in the 1970s and very slow growth since then. However, DIC for this model was −134.0, indicating a poor fit to the data, similar to that of the model with both θ and Z constant over time (Table 2). Like the latter model, this model tended to overestimate juvenile abundance in the early 1970s, underestimate juvenile abundance throughout the 1980s and 1990s, and underestimate adult abundance in the 1970s (compare Fig. 3a, b and Fig. 10d, e). When both θ and Z were allowed to vary on a decadal scale with vague priors (model Δ$G3$), posteriors for the Z parameters indicated a decline in juvenile mortality and an increase in adult mortality similar to that observed assuming constant θ (Fig. 10l, m). Posterior distributions for θ were similar to the priors and did not indicate decadal variation in this parameter (Fig. 10k). DIC was −163.0, reflecting a model fit (Fig. 10n, o) similar to that of the models with variable Z but constant θ (Table 2, Fig. 3c, d). Similar changes in mortality persisted when decadal variation in θ was imposed by using informative priors for θ (model Δ$G2$, Fig. 10f–j, DIC = −162.6).

DISCUSSION

Causes of winter skate declines

The Committee on the Status of Endangered Wildlife in Canada (COSEWIC) considered the probable cause of declining winter skate abundance to be unsustainable rates of bycatch in fisheries targeting other groundfishes (COSEWIC 2005). Our analyses indicate that an increase in the natural mortality of adult skates also contributes to these declines. Evidence is strongest for the southern Gulf of St. Lawrence (SGSL), where the declines in skate abundance have been the most dramatic. In this area, the estimated trend in fishing mortality was opposite to the trend in total adult mortality (Fig. 4), indicating that increases in total mortality were likely due to increases in natural mortality. This population has continued to decline despite the reduction of estimated exploitation rates to very low levels since the early 1990s. Exploitation appears to have played a more important role in the decline of winter skate on the eastern Scotian Shelf (ESS). In this area, estimated rates of both natural mortality and exploitation increased for adults in the 1990s. High exploitation rates on the ESS in the mid 1990s reflected the opening of a directed fishery for winter skate in this area. Catches in this fishery declined to low levels in the 2000s, as have estimated exploitation rates.

Our estimates of mortality rates are influenced by prior information (i.e., the prior on the transition probability θ) and, for the SGSL population, catchability adjustments (i.e., day catchability vs. night catchability). However, temporal patterns in mortality were insensitive to these factors. In particular, the hypothesis that the estimated increase in adult mortality in the 1980s and 1990s might be an artifact of reduced juvenile growth during these periods could be rejected; increases in estimated mortality persisted when the widest plausible variation in juvenile growth was allowed or imposed in models of the SGSL population. Preliminary aging data for this population are also inconsistent with this hypothesis; these data indicate that growth is not currently slow (D. P. Swain, *unpublished data*).

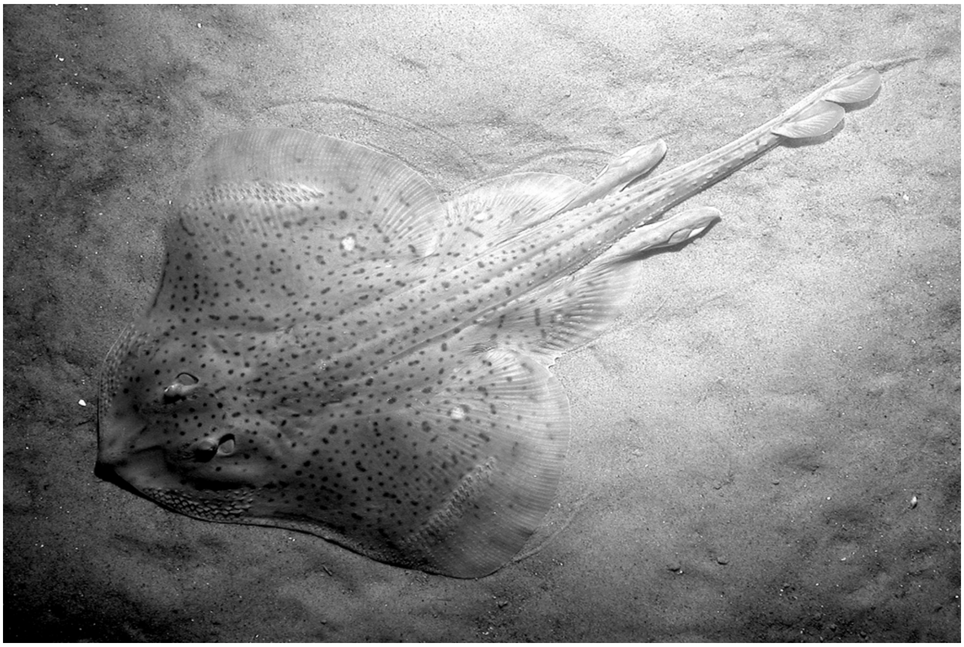

PLATE 1. Mature male winter skate (*Leucoraja ocellata*), eastern Scotian Shelf, Atlantic Canada. Photo courtesy of the Photo Unit, Bedford Institute of Oceanography, Fisheries and Oceans Canada.

The length-dependent changes in natural mortality observed in winter skate, with mortality decreasing for juvenile skate and increasing for adult skate, are consistent with ecosystem-wide changes in these areas. In both areas, abundance of small-bodied fishes increased in the late 1980s and early 1990s (Choi et al. 2005, Benoît and Swain 2008), suggesting decreases in the mortality of these fishes. In contrast, mortality of large demersal fishes in the SGSL remained high in the 1990s despite dramatic declines in fishing mortality, indicating increases in natural mortality for these fish (e.g., cod, Sinclair 2001; white hake, Hurlbut and Poirier 2000).

Skates are a component of seal diets (Benoit and Bowen 1990, Hammill and Stenson 2000). Their contribution to seal diets appears to be minor, but is likely underestimated because they lack the bony parts normally used to identify the fish prey of seals (Pierce and Boyle 1991). Natural mortality of adult skate was positively related to the abundance of grey seals (*Halichoerus grypus*), particularly in the SGSL. A similar correlation has been noted for adult cod in this ecosystem (Chouinard et al. 2005). These correlations are consistent with the hypothesis that increased predation by the expanding grey seal herd contributes to the increased natural mortality of large demersal fish in this ecosystem. This hypothesis is, however, inconsistent with the view that grey seals feed primarily on small fish (Hammill and Stenson 2002). This view is based on the size distribution of otoliths (bones in the heads of teleost fishes) recovered from seal stomachs and scats, and may be biased toward small sizes if seals frequently do not consume the heads of large fish (see discussion in Chouinard et al. [2005]).

Recent increases in the abundance of small-bodied fishes in the SGSL and on the ESS are thought to reflect release from predation following collapses in the abundance of large demersal fish (Choi et al. 2005, Benoît and Swain 2008). These increases in the abundance of small fish have occurred despite sharp increases in the abundance of grey seals in both ecosystems. This may reflect the difference between large demersal fish and grey seals in total consumption in these ecosystems. In the SGSL, estimated consumption by grey seals and adult cod was 0.5 and 8.2 $\mathrm{Mg \cdot km^{-2} \cdot yr^{-1}}$, respectively, in the mid 1980s and 1.0 and 3.5 $\mathrm{Mg \cdot km^{-2} \cdot yr^{-1}}$, respectively, in the mid 1990s (Savenkoff et al. 2004). Thus, the expected net effect of the changes in abundance of large demersal fish and grey seals is a decrease in predation on small fish (consumed by both seals and large demersal fish) and an increase in predation on large fish (consumed only by grey seals).

Relationships between juvenile skate mortality and predator abundance were not consistent with expected effects. Grey seal abundance and estimated mortality of juvenile skates in the SGSL were negatively correlated, opposite to the expected relationship. The relationship between cod abundance and juvenile mortality was in the expected direction (in univariate analyses) but the posterior distribution of the slope parameter broadly overlapped zero. This may partly reflect the difficulty in statistically disentangling the confounded effects of changes in seal and large cod abundance ($R = -0.61$ and -0.64 for the SGSL and ESS, respectively). The indices of predator abundance may also fail to capture important aspects of the interaction between skates and their predators. For example, the distribution of cod during their feeding season in the SGSL shifted offshore in the late 1970s and early 1980s (Swain 1999). Thus, predation by cod on winter skate (which are restricted to shallow inshore waters during the feeding season) would be expected to begin to decline in the 1970s prior to the decline in the abundance of large cod in the mid to late 1980s, an effect not captured by our index of predation based solely on the abundance of large cod.

The inshore temperature index was the factor most strongly related to the natural mortality rate of juvenile skate in the SGSL, with mortality decreasing as temperature increased. The significance of this relationship is unclear. Natural mortality of juvenile skate on the ESS was unrelated to water temperature. Furthermore, temporal trends in natural mortality were similar between juvenile skate in the SGSL and the small juvenile size class on the ESS, even though there was no similarity between the temperature trends experienced by the two groups. This suggests that the correlation between temperature and natural mortality of juveniles in the SGSL may be spurious.

Mortality trends were similar between the SGSL and the ESS in that mortality decreased in both areas for the smallest length classes considered and increased in both areas for adult skates. This is generally consistent with the hypothesis that predation mortality decreased on small skates with collapses in the abundance of large demersal fish in both areas and increased on large skates as the grey seal herds expanded in both areas. However, the length ranges of the groups with decreasing or increasing mortality differed between the two areas. In the SGSL, mortality decreased for skates 20–41 cm in length and increased for those 42 cm or longer. On the ESS, mortality tended to decrease for skates 36–59 cm in length (the smallest length class considered) and to increase for those 75 cm or longer. This suggests that the increase in mortality of adult skates may be related to maturation rather than to size-dependent predation. Further work on the causes of changes in natural mortality of winter skate in these two ecosystems is needed.

Recovery potential

Population projections indicate that, even with no fishery removals, recovery of these populations is unlikely at their current levels of natural mortality. Abundance of the ESS population is expected to stabilize at a low level if all fishery removals are eliminated, but the SGSL population appears to be no longer viable and is expected to continue to decline even in the absence of fishery removals. Uncertainty around projected abundance is high, but does not include recovery in the case of the SGSL population. If predation by seals is an important component of the elevated natural mortality of adults, then these projections are overly optimistic given the continuing increase in grey seal abundance.

Caveats

We have attempted to quantify fishery removals from all sources, including both landings and discarded bycatch. However, no information existed for some potential sources of fishing mortality, in particular clam and scallop fisheries on the ESS and scallop fisheries in the SGSL. Fishing mortality from these sources would contribute to estimated natural mortality in our models. Scallop landings in the SGSL declined sharply in the early 1970s, remained roughly stable from the mid 1970s to the early 1990s, increased somewhat in the mid 1990s, and then declined to a low level in recent years (Swain et al. 2006). Thus, changes in bycatch in the scallop fishery might contribute to the apparent decline in juvenile skate mortality in the SGSL between the 1970s and 1980s, but do not appear to provide an explanation for the increased adult mortality in the 1980s and 1990s. Preliminary information suggests that bycatch mortality of winter skate in the SGSL scallop fishery is very low (L.-A. Davidson, M. Lanteigne, and H. P. Benoît, *personal communication*) but work is on-going to obtain estimates of this mortality.

The July survey of the ESS covers most of the habitat occupied by winter skate on the offshore ESS banks in summer, but a portion of the SGSL population occurs inshore of the area covered by the September survey. This leads to the concern that SGSL abundance indices may be biased by changes in availability to the survey. In particular, if winter skate distribution is density dependent, expanding into marginal habitat as abundance increases (MacCall 1990), and optimal habitat for winter skate occurs inshore of the survey area, then availability of winter skate to the SGSL survey is expected to be higher when abundance is high. In this case, changes in survey catch rates will overestimate changes in population abundance. However, preliminary analyses assuming that density-dependent changes in winter skate distribution follow the ideal free distribution (Fretwell and Lucas 1970) suggest that the bias in estimated population decline due to this cause is slight (i.e., 95% vs. 98% declines over the 1971–2004 period; D. P. Swain, *unpublished data*). Moreover, a bottom-trawl survey conducted since 2000 in areas inshore of those covered by the September survey confirms that winter skate abundance is declining sharply in these inshore areas also (Swain et al. 2006).

Our population models incorporate many simplifying assumptions. In particular, juvenile growth rate and length at maturity are assumed to be constant over time, and maturation is assumed to be knife edged. Our main conclusion, that juvenile mortality has declined and adult mortality increased, was insensitive to violation of the assumption of time invariant growth rate. Sensitivity to the other assumptions was not examined. However, the assumption of constant length at maturity is supported by the available data. For both the SGSL population and populations outside of the Gulf, no differences in length at maturity are evident between the 1960s and early 1970s (McEachran and Martin 1977: Fig. 1) and recent years (Simon et al. 2003, Frisk 2004, McPhie 2007; J. M. Hanson, *personal communication*). Finally, the common assumption of knife-edged maturation generally has little effect on model outputs. For example, in population models of Gulf menhaden, differences in estimated fishing mortality and recruit abundance were negligible between models assuming knife-edged or gradual maturation (Vaughan et al. 2007).

Modeling methodology

Modeling is needed to assess the risks to threatened populations, to predict outcomes of alternative management scenarios, and to assess uncertainty associated with the predicted outcomes. Fisheries stock assessment models are often structured by age, requiring detailed age-disaggregated data and ancillary information (e.g., McAllister and Ianelli 1997, Quinn and Deriso 1999). More highly aggregated models such as surplus production and delay-difference models, can be used when less detailed data are available (Deriso 1980, Schnute 1984, Prager 1994), though age-aggregated data may be uninformative about key model parameters (McAllister et al. 2001). In general, the commonly used stock assessment approaches are data hungry and make strong assumptions about population structure and process.

In conservation biology, information on the life history of a species often is less well-known and data can be sparse. Approaches here tend to make fewer assumptions about the population dynamics by fitting random walk or diffusion approximation models to estimate long-term population growth rates and various metrics of extinction risk in the presence of environmental stochasticity (Lande and Orzack 1988, Dennis et al. 1991, Holmes et al. 2007) or multiple sources of uncertainty (Lindley 2003). Alternatively, Leslie matrix models (Caswell 2001) are used to conduct population viability analyses. These models require estimates of vital rates, such as age-specific fecundities and survival probabilities, typically obtained from short-term field studies on the modeled population or from previous studies of related populations or species. In this approach, population viability and risk are assessed using stochastic simulation, with vital rates sampled from specified probability distributions (e.g., Ratner et al. 1997). It is rare, however, that matrix population models are embedded in a statistical inference framework that allows data to inform the parameterization of the population model and that allows an evaluation of uncertainty in the parameters, observations, process, and model choice (Tuljapurkar 1997, Buckland et al. 2007).

Our Bayesian state–space approach to modeling winter skate dynamics is similar to methods used for catch-at-length stock assessments (Sullivan 1992, Punt and Kennedy 1997); however, our length classes are necessarily far coarser due to the limited available data and life history information. Sullivan (1992) and Schnute (1994) used a Kalman filter state–space approach that simultaneously accounted for both process variability and observation error but restricted analysis to linear models, or linear approximations of nonlinear models, and normally distributed process variability and observation errors. Bayesian state–space models can handle nonlinear dynamics and non-normal errors and these methods have gained popularity with a variety of applications in resource management and conservation biology (Meyer and Millar 1999, Buckland et al. 2007).

The stage-structured population model presented here was tailored for the available winter skate monitoring and fishery catch data. By embedding the size-structured population model within a Bayesian state–space framework, we were able to (1) formally incorporate published life history data as priors to inform the estimation of parameters for which the monitoring data contain little or no information, and (2) account for parameter uncertainty, process variability, and observation error (but see deValpine and Hastings [2002]). This approach is an example of the more general Bayesian state–space or hidden process model methods advocated by others (Schnute 1994, Gross et al. 2002, Clark and Bjornstad 2004, Newman et al. 2006, Buckland et al. 2007).

An important aspect of our particular approach is the assumption of variability in mortality rates through time. Age-aggregated monitoring data contain little or no information on natural mortality, and estimation of total mortality often is overwhelmed by observation error and variability. By estimating mortality as a function of the unobserved states and additional data on commercial landings and/or discarding at sea, we were able to account for observation error and unassociated process variability. Trends in mortality were estimated by allowing the mortality terms (Z or M) to be a function of time or environmental covariates. Non-stationary matrix models can be used to assess influences of changing vital rates (Gotelli and Ellison 2006), but these require field estimates of vital rates and experimental data on environmental effects on these rates, information that is lacking for most populations of conservation concern. Even data-rich fisheries applications generally assume that rates of population productivity, in particular natural mortality, are constant, though some recent applications assume or estimate changes in these rates (e.g., Chouinard et al. 2005).

We used deviance information criterion (DIC) to perform model selection; however, this approach is the subject of some controversy among statisticians (see discussion after Spiegelhalter et al. [2002]). It is possible that alternate conclusions would be made regarding the form of trends in total or natural mortality and their relationships with the environmental covariates had a different model selection method been used. Other model selection methods, such as minimum posterior predictive loss (Gelfand and Ghosh 1998) or reversible jump Markov Chain Monte Carlo (King and Brooks 2001) could be used. In the latter case, the model is treated as an additional parameter and the joint posterior distribution is computed over both the parameter and model space (Gimenez et al. 2009). The posterior probability for each model can be used as a selection criterion or as model weights (e.g., Link and Barker 2006) and Bayesian model averaging can be performed to assess model uncertainty (King and Brooks 2001). However, it is not likely that our main conclusion, that juvenile natural mortality has declined and adult natural mortality has increased, would be altered using these more sophisticated model selection approaches, at least for the SGSL population.

Conclusions

Time series of size distributions are available for most marine fish populations monitored by research surveys. Stage-structured models of the type described here can be used to extract information from these time series in order to estimate vital rates and changes in these rates. In the winter skate examples described here, these models revealed unexpected changes in natural mortality and led to a revised view of the threats to these populations and the causes of their decline.

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APPENDIX A

Geographic distribution of winter skate catches in September trawl surveys of the southern Gulf of St. Lawrence and July surveys of the eastern Scotian Shelf (*Ecological Archives* A019-055-A1).

APPENDIX B

Catchability and availability of winter skate to annual trawl surveys of the southern Gulf of St. Lawrence and eastern Scotian Shelf (*Ecological Archives* A019-055-A2).

APPENDIX C

Prior information on the population dynamics of winter skate in the southern Gulf of St. Lawrence and on the eastern Scotian Shelf (*Ecological Archives* A019-055-A3).

APPENDIX D

Example model code (*Ecological Archives* A019-055-A4).

APPENDIX E

Prior and posterior distributions for selected models (*Ecological Archives* A019-055-A5).

APPENDIX F

Initial values of parameters in Z- and M-models (*Ecological Archives* A019-055-A6).

APPENDIX G

Convergence statistics for selected models (*Ecological Archives* A019-055-A7).

APPENDIX H

Mortality rates of winter skate in the southern Gulf of St. Lawrence and on the eastern Scotian Shelf, estimated by models assuming a random walk or temporal trend in mortality (*Ecological Archives* A019-055-A8).

SUPPLEMENT

Data used to estimate mortality rates of winter skate in the southern Gulf of St. Lawrence and on the eastern Scotian Shelf (*Ecological Archives* A019-055-S1).