Identifying nonproportionality of fishery-independent survey data to estimate population trends and assess recovery potential for cusk (*Brosme brosme*)

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Abstract: Cusk (*Brosme brosme*) was designated as "threatened" by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) in 2003, based on an estimated 93% decline between 1970 and 2001 from the Fisheries and Oceans Canada (DFO) Scotian Shelf summer bottom trawl survey index. We combined this index with a fishery-dependent longline index in a Bayesian surplus production state-space model to estimate population trends and the recovery potential of western Scotian Shelf cusk. We tested for index nonproportionality using a power curve function in the observation model and identified potential hyperdepletion for cusk in the trawl survey index. We estimate a 59% decline in cusk biomass between 1970 and 2001, and a 64% decline from 1970 to 2007. Although population projections indicate the current landing limit should lead to population recovery, robustness tests suggest the biomass projections and recovery time lines are overly optimistic. Simulations showed that incorporating multiple indices increases power to recapture model parameters and failure to account for index nonproportionality results in biased parameter estimates. We suggest that nonproportionality of fishery-independent indices must be considered when determining the population status of data-poor species.

Résumé : Le brosme (*Brosme brosme*) a été désigné espèce menacée par le Comité sur la situation des espèces en péril au Canada (COSEPAC/COSEWIC) en 2003 en se basant sur un déclin estimé de 93 % de 1970 à 2001 d'après l'indice de l'inventaire par chalutage de fond en été sur la plate-forme Néo-écossaise de Pêches et Océans Canada (MPO/DFO). Nous combinons cet indice avec un indice basé sur la pêche commerciale à la palangre dans un modèle bayésien état-espace de production excédentaire afin d'estimer les tendances de la population et le potentiel de récupération des brosmes de l'ouest de la plate-forme Néo-écossaise. Nous avons vérifié l'absence de proportionnalité de l'indice à l'aide d'une fonction de courbe de puissance dans le modèle d'observation et avons décelé un épuisement exagéré dans l'indice basé sur l'inventaire au chalut. Nous estimons un déclin de 59 % de la biomasse des brosmes de 1970 à 2001 et un déclin de 64 % de 1970 à 2007. Bien que les projections démographiques indiquent que la limite actuelle des débarquements devrait permettre une récupération de la population, des tests de robustesse montrent que les projections de biomasse et les échéanciers de récupération sont trop optimistes. Des simulations révèlent que l'incorporation de plusieurs indices augmente le pouvoir de récapture des paramètres du modèle et que la négligence de l'absence de proportionnalité des indices entraîne une erreur dans l'estimation des paramètres. Nous suggérons qu'il est nécessaire de tenir compte de l'absence de proportionnalité dans les indices indépendants de la pêche quand on détermine le statut d'espèces pour lesquelles on possède peu de données.

[Traduit par la Rédaction]

Introduction

Fisheries stock assessments are frequently based on data intensive population dynamics models, and thus are generally limited to the target species of large-scale commercial fisheries (Davis 2002; Kelly and Codling 2006). On the east coast of Canada, for example, stock assessments have been conducted for fewer than 5% of all marine fish species (Hutchings and Baum 2005). Detailed life-history information and appropriate long-term catch and monitoring data re-

quired for such assessments are typically lacking for incidentally caught species (McAllister et al. 2001; Hall and Mainprize 2005). These species may, however, experience significant incidental mortality as bycatch (Crowder and Murawski 1998; Baum et al. 2003), and it is therefore essential that quantitative estimates of the impacts of exploitation on them are developed.

Cusk (*Brosme brosme*) is a data-poor benthic teleost (Family Gadidae) of the north Atlantic, which is commonly

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414

Can. J. Fish. Aquat. Sci. Vol. 68, 2011

caught as bycatch in benthic longline and lobster fisheries (DFO 2004). Little is known about its life history and ecology; however, catch rates in eastern Canada's groundfish longline fishery suggest cusk prefer rocky complex habitat in relatively deep water (400–600 m, Oldham 1966; Harris et al. 2002). Life history parameters including growth rate, natural mortality, and maximum age are unknown. Cusk is principally a bycatch species in Canada and the US, but is frequently retained prior to landing limits being reached. In Canada, landings were unregulated until 1999, after which a limit of 1000 t was imposed for the majority of the Scotian Shelf (4VWX Northwest Atlantic Fisheries Organization (NAFO) divisions). Owing to increased conservation concerns, this limit was reduced to 750 t in 2003 and extended to include the Canadian portion of Georges Bank (5Zc, DFO 2008).

Cusk was designated as "threatened" by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) in 2003, based on an estimated 93% decline between 1970 and 2001 in the Fisheries and Oceans Canada (DFO) Scotian Shelf summer bottom-trawl survey index (COSEWIC 2003). This estimate has been contested by DFO scientists because the trawl survey samples outside the preferred habitat and depth range of cusk, and therefore, the survey index may not be proportional to cusk population abundance (DFO 2004). The assumption that catch rate indices are proportional to abundance is commonly made in population models, and was used in the COSEWIC assessment, despite the fact that it rarely holds (Richards and Schnute 1986; Harley et al. 2001; Maunder et al. 2006). Nonproportionality has been recognized to occur in commercial catch-rate data (Harley et al. 2001); however, fishery-independent data can also suffer from nonproportionality if a large component of the stock is found outside the survey area (Blanchard et al. 2008). Failure to account for nonproportionality when present, in either commercial catch rate or fishery-independent data, can result in biased estimates of stock decline.

The objectives of our research were to estimate historical population trends, current status, and the recovery potential of western Scotian Shelf cusk (NAFO division 4X; Fig. 1) by using two indices of relative biomass and evaluating each of them for nonproportionality. We incorporated a fishery independent bottom-trawl survey index and a fishery dependent catch-per-unit-effort (CPUE) benthic longline index within a Bayesian state-space surplus production model, and used a power curve function in the observation model to test for nonproportionality of the indices. We then used the model-derived biomass and parameter estimates in stochastic simulations to project biomass forward and assess recovery potential based on three different landing limits. Finally, we used a simulation approach to evaluate consequences of model misspecification and the advantages of using both indices to obtain unbiased parameter estimates.

Materials and methods

Data

Time-series data for cusk on the western Scotian Shelf include annual reported landings and two catch rate indices of relative biomass (Fig. 2). One index is a fishery-independent

Fig. 1. Location of study. Bold unbroken line is the 4X major Northwest Atlantic Fisheries Organization management unit area. Dashed lines are the minor management units from which the commercial longline index is derived. Ragged dashed line is the 500 m isobath.
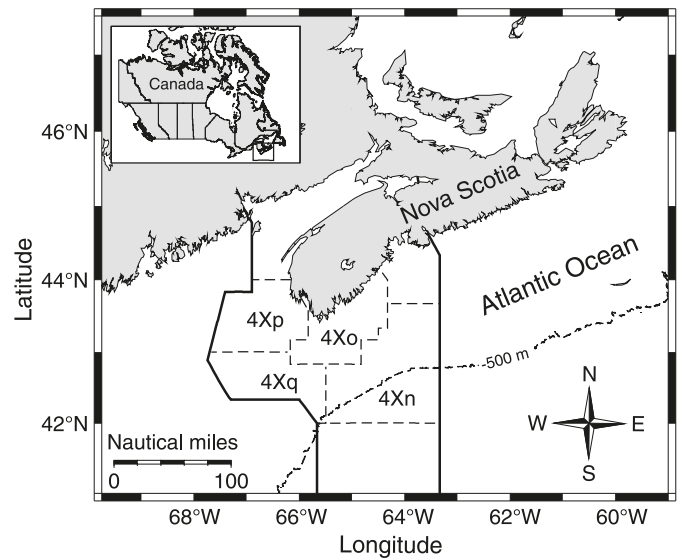

index based on the DFO summer bottom-trawl survey, and the second is a fishery-dependent index derived from the commercial groundfish longline fishery, in which cusk is bycatch. Owing to insufficient data on unreported and incidental mortality, we make the assumption that reported landings are synonymous with fishery removals and are known without error. The DFO summer bottom-trawl survey covers most of the Scotian Shelf and has been conducted each July since 1970. The survey follows a stratified random design with stratification based on depth and geographic area (Shackell and Frank 2003). The stratified mean catch per standard 1.75 nautical mile tow (1 international nautical mile = 5.56 km) is used as an index of relative biomass. We restricted the index to only include the western Scotian Shelf (4X NAFO division) so that it would cover the same region as the commercial catch rate index. Cusk catch rates in the survey have always been low because the rocky complex habitat preferred by cusk (Oldham 1966) is poorly sampled by the survey trawl gear.

The CPUE index from the commercial groundfish longline fishery covers most of the western Scotian Shelf (4Xnopq NAFO subdivisions) and spans from 1986 to 2007. We focused on this fishery because it has the highest cusk catches in Atlantic Canada (>95% of all cusk landings on the Scotian Shelf and Georges Bank since 1990). Catches from areas of marginal cusk habitat, such as the Bay of Fundy and shallow inshore regions, were not included. The index was restricted to vessels of 25 to 149.9 gross registered tons, since no effort information was available for smaller longliners in early parts of the time-series. To avoid introducing bias from landing limits being reached, we restricted the commercial catch rate index to the first 3 months of each year's fishing season (July to September).

Reported landings and the commercial index may be biased high in the time series.. The lack of a landings limit for cusk prior to 1999 could, for example, have resulted in

Fig. 2. Time-series of fishery independent bottom trawl (filled circle, ●), and commercial longline catch-per-unit-effort (filled triangle, ▲) indices for cusk from the 4Xnopq NAFO subdivisions. Recorded landings (bars) are from the 4X NAFO division.
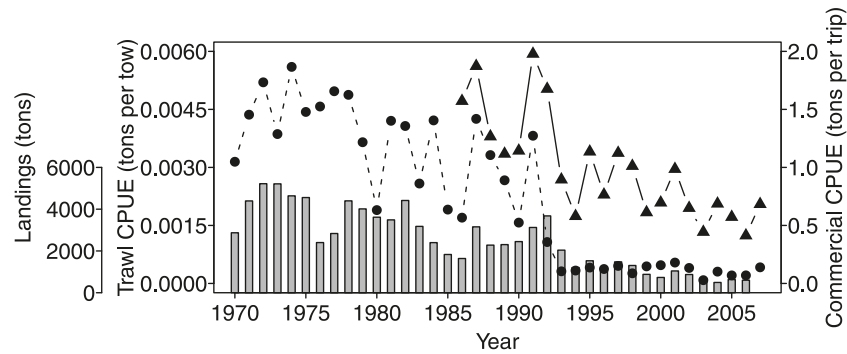
target-species such as cod (*Gadus morhua*) being reported as cusk when cod quotas were exceeded, thus potentially inflating the cusk landings and commercial catch rates. Because the level of misreporting could not be quantified, we did not apply corrections to either time series. However, the level of misreporting, if present, in the longline fishery index prior to 1999 appears minor, as the index follows the yearly catch rate dynamics in the fishery-independent trawl index over the same period (Fig. 2).

The lack of age or length disaggregated data for both indices limited our choice of population models and our ability to track year class variability and population age-structure. Although age and length disaggregated information exists for the trawl survey time-series, commercial data was limited to yearly biomass and effort, and landings simply as biomass. If catch-at-age/length data were available for all the data series, we could have compared the catch rates of each size class over time to better understand the relationship of each time-series to population abundance.

Population model

Recognition of the importance of both observation error and process variability has increased the application of state-space models in the assessment of fish and endangered species in the last decade (Harwood and Stokes 2003; Clark and Bjørnstad 2004). State-space models differ from traditional deterministic population models in that they consist of two components: a process model, which represents the unobservable stochastic processes governing the population dynamics, and an observation model, which describes the error structure inherent in the observations (Meyer and Millar 1999*b*; Harwood and Stokes 2003). By coupling these components in a state-space framework, the errors in the observations can be separated from natural variability in the population processes. We employed a Schaefer surplus production model (Schaefer 1954) as our process model, because there was insufficient age-disaggregated and life history data to use more complex age-structured models. Surplus production models are commonly employed when indices of relative biomass and landings are the only data available for population assessment (Hilborn and Walters 1992). Implicit assumptions of the Schaefer model are a symmetrical surplus production curve where maximum surplus production (MSP) occurs at 50% of unfished biomass, and a population at equilibrium (Schaefer 1954; Hilborn

and Walters 1992). The Schaefer surplus production model is

$$(1) \qquad B_t = \left(B_{t-1} + rB_{t-1}\left(1 - \frac{B_{t-1}}{K}\right) - C_{t-1} \right)\eta_t$$

where B_{t-1} and C_{t-1} denote biomass and catch (landings), respectively, for year $t-1$. Carrying capacity, K, is the biomass of the population at equilibrium prior to commencement of the fishery; r is the intrinsic population growth rate; and η_t is a lognormal random variable with a mean of zero and variance σ^2 to account for stochasticity in the population dynamics. Recruitment, growth, and natural and unreported fishing mortality are combined in the time-invariant parameter, r. All parameters are held constant over time (i.e., changes in the biotic and abiotic environment are not included) and catchability is the same for all individuals in the population.

The observation model relates the unobserved states, B_t, to the indices of relative biomass, $I_{i,t}$, that are observed with error. We incorporate both the trawl survey index and longline index in a single model by specifying a separate observation equation for each. A commonly used observation model is

$$(2) \qquad I_{i,t} = q_i B_t \varepsilon_{i,t}$$

where $I_{i,t}$ is the relative abundance of index i at time t; q_i is the catchability coefficient for index i, which describes the effectiveness of each unit of fishing effort; and $\varepsilon_{i,t}$ is a lognormal random variable with a mean of zero and variance τ_i^2 to account accounting for error in the observations of index i.

A critical assumption of eq. 2 is that the catch rate indices are assumed to be proportional to biomass, regardless of population size (i.e., constant q). Because our data are spatially aggregated and have no age-disaggregation, the catchability parameter is a conglomeration of the three different processes governing the effectiveness of the fishing gear: availability, catchability, and selectivity. Density dependent habitat selection exhibited as range contraction to optimal habitat areas as abundance declines is observed in many exploited fish stocks (Blanchard et al. 2008). We hypothesize that as cusk biomass declined, remaining individuals retreated to optimal habitat areas where they remained available to the longline fleet but were less available to trawl gear, which is restricted to noncomplex substrate that is con-

416

Can. J. Fish. Aquat. Sci. Vol. 68, 2011

sidered to be poor cusk habitat. Unfortunately, spatially dis-aggregated catch rate data for the commercial fleet was un-available to directly test this hypothesis. Rather, to account for this potential change in cusk availability to the trawl gear, we relaxed the assumption of constant catchability by adding a shape parameter to the observation model. This power curve relationship between the catch rate indices and population biomass allows catchability to change as popula-tion biomass changes. Catchability then becomes a function of q and β (catchability = $qB^{\beta-1}$, Harley et al. 2001). Our observation model becomes eq. 3:

$$(3) \qquad I_{i,t} = q_i B_t^{\beta_i} \varepsilon_{i,t}$$

where β_i is a shape parameter for index i.

Equation 3 reduces to eq. 2 when $\beta = 1$. In the context of population declines, $\beta < 1$ implies the catch rate index de-clines more slowly than population biomass, a condition known as hyperstability (Fig. 3). Hyperstability occurs in many commercial catch rate indices (Harley et al. 2001) and can be the result of the nonrandom search behaviour of fishers and (or) schooling behaviour or range contraction of target species (Rose and Kulka 1999). Assuming proportion-ality of a hyperstable index can result in underestimates of exploitation rate and total population decline (Hilborn and Walters 1992). Conversely, hyperdepletion occurs when $\beta > 1$ and describes the situation where the catch rate declines faster than population biomass (Fig. 3). This can occur when fishing effort is concentrated on a subset of the popu-lation that may be depleted, while a significant subset of the population remains unaccounted for in the catch rate index (Quinn and Deriso 1999). For example, the fixed area design of fishery-independent surveys can potentially result in a hy-perdepleted catch rate index if the core density of a species is outside the survey area and species specific processes such as density dependent habitat selection results in incom-plete mixing of the population within its full range (Blan-chard et al. 2008). Assuming a hyperdepleted index is proportional to biomass can result in overestimates of popu-lation decline and exploitation rate (e.g., Myers and Worm (2003) as pointed out by Walters (2003), Maunder et al. (2006) and Sibert et al. (2006)).

Four variants of the observation component of the surplus production model were compared: (*i*) both indices fixed to be proportional to biomass (i.e., $\beta = 1$); (*ii*) shape parame-ters estimated for both indices; (*iii*) the longline index fixed to be proportional to biomass and a shape parameter esti-mated for the trawl index; and (*iv*) the trawl index fixed to be proportional to biomass and a shape parameter estimated for the longline index.

We implemented the state-space models in WinBUGS (version 1.4.3, Lunn et al. 2000) via the R2WinBUGS pack-age (Sturtz et al. 2005) in the statistical programming envi-ronment R (R Development Core Team 2008). WinBUGS uses a Markov Chain Monte Carlo (MCMC) approach to es-timate the joint posterior distribution of the model parame-ters. Marginal posterior distributions of model parameters and unobserved states were based on 300 000 iterations of two chains after discarding the first 260 000 iterations (burn-in). These 40 000 iterations were reduced to 2000 by

Fig. 3. Three possible power curve relationships of catch-per-unit-effort and biomass. Figure adapted from Hilborn and Walters (1992).
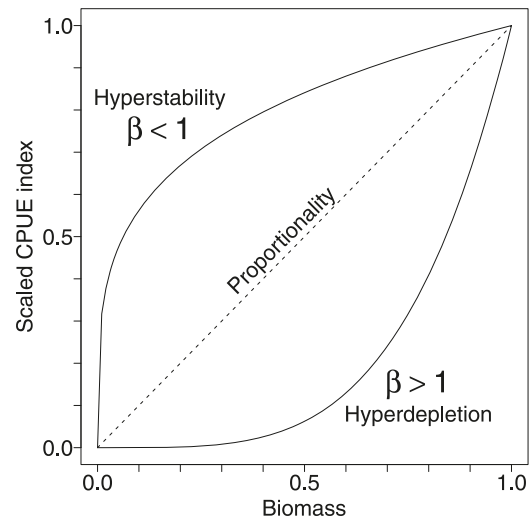
sampling every 20th value to reduce sample autocorrelation. Models were considered to have converged when the poten-tial scale reduction factor $\widehat{R}$ was <1.2 for all parameters (Brooks and Gelman 1998). See online supplementary data[2], Appendix S1 for WinBUGS code.

Priors

A potential advantage of the Bayesian approach is that other sources of information can be incorporated into the analysis in the form of priors (Gelman et al. 2004). Unfortu-nately, since little is known about cusk ecology or its catch-ability on trawl or longline gear, we were limited to relatively broad flat priors (Table 1). We specified a vague prior for carrying capacity, K, using a uniform distribution with a lower boundary of the maximum reported landings of 5219 t and an upper boundary of 500 000 t. Although the upper boundary is greater than reasonable predictions for K, it was used to ensure that some probability density would be present in unlikely, although possible estimates of K. The purpose of this prior was to restrict the parameter search away from mathematically possible yet biologically implau-sible parameter combinations (e.g., a high estimate for r coupled with an extremely low estimate for K). We made the assumption that the cusk population at the beginning of the trawl index (1970) was equal to K with an error distribu-tion equal to the estimated process error, because the trawl catch rate was relatively stable from 1970 to 1980, and esti-mating, rather than specifying B_0, increases confounding in the model parameters (Hilborn and Walters 1992). Further-more, the low contrast and "one-way-trip" trends exhibited by both the survey and commercial data make estimating B_0 as a free parameter difficult. Estimates of absolute decline therefore need to be viewed in the context of this assump-tion.

We considered including an informative prior for the shape parameter, β. Harley et al. (2001) obtained maximum-likelihood estimates of shape parameters for commercial

[2] Supplementary data for this article are available on the journal Web site (http://cjfas.nrc.ca).

Table 1. Summary of specified priors for Bayesian state-space model.

Parameter	Prior
r (intrinsic growth rate)	Uniform(0,4)
K (carrying capacity; tons)	Uniform(5219, 500 000)
σ^2 (process error variance)	Uniform(0, 100)
τ^2 (observation error variance)	Uniform(0, 100)
q (catchability coefficient)	Uniform(0,1)
β (shape parameters)	Uniform(0.01,10)

catch rate indices of flatfish, cod, and other gadiformes, and found strong evidence of hyperstability in many indices. This property likely arose because of the searching and targeting behaviour of fishers for these target species (Hilborn and Walters 1992). We did not incorporate their findings into our analyses because cusk is taken primarily as bycatch, and there was weak a priori reason to expect hyperstability in the commercial catch rate index.

Model selection and sensitivity

We used two methods for model selection and to evaluate model fit. First, we utilized the estimated deviance information criterion (DIC), which penalizes model complexity and a lower score identifies a better model fit. Second, we conducted a retrospective analysis by omitting the last 7 years of the biomass indices (but retained the landings data) and checked the model's ability to predict the missing data by projecting the model forward 7 years (e.g., Gelman et al. 2004; Snover 2008). The decision to omit 7 years was largely arbitrary; however, we felt that 7 years was a good balance between retaining enough data for representative model fits and evaluating the predictive ability of the model. We used this approach to determine how well each model could predict future states and to assess the robustness of the parameter estimates. This approach also had the added benefit of evaluating the robustness of the recovery scenarios under different future catch rates. Lastly, we evaluated the sensitivity of parameter estimates to alternative specifications of the r and error variance priors for the model that received the most support according to the two criteria described above to ensure that the Bayesian analysis was not driven by the priors (McAllister et al. 2001). Therefore, we re-fit Model 3 with either lognormal priors with a mean of 0.25 or 1.0 and a variance of 1.0 for r and normal priors with a mean and variance of 1.0 for the process and observation error variances (σ^2, τ_L^2, and τ_T^2).

Biomass projections

Biomass was projected into the future to evaluate whether the current landing limit of 750 t is sufficient to allow for population recovery. Because the error associated with the observation process has no effect on the true population biomass, the state-space approach can be particularly useful when generating biomass projections using model derived population parameters. Indeed, if observation error is significant, and simply combined with process error, the uncertainty of population projections can be overestimated and potentially biased (Dennis et al. 2006).

Three catch landings levels were evaluated: 0, 750, and 1500 t per year. Projections were done in R using a stochas-

tic simulation approach with the retained MCMC parameter realizations (B_{2007}, r, K, σ) from the joint posterior probability distribution of the model that assumed the longline index was proportional to biomass but estimated a shape parameter for the trawl index (Model 3 because this model received the most support according to the criterion described above). We changed modeling platforms for the projections due to the lack of programming flexibility in WinBUGS and because the lognormal distributional assumption of the population in the retrospective model can become invalid at unsustainable specified catch levels. We generated five process error deviated biomass realizations per year using the retained associated parameter realizations (n = 4000 after burn-in and thinning; for a total of 20 000 biomass estimates per year). Population realizations were fixed to zero once they became extinct.

The equilibrium assumption of the Schaefer model means that a change in exploitation rate will result in an immediate change in the population growth rate, thus potentially omitting important ecological processes such as recruitment time-lags and changes in population growth rate resulting from an altered age structure. Consequently, projections will likely overestimate biomass increases in response to reductions in fishing mortality.

Simulations

We used a simulation approach to investigate the consequences of model misspecification on the parameter and biomass estimates, and to quantify the advantage of including both indices of relative biomass, rather than just one (Table 2). To retain features of our best estimates of the true biomass trajectory, the landings data, and index histories for this particular stock, we employed a method akin to a parametric bootstrap by taking the median biomass estimates obtained from Model 3 as the true biomass trajectory for our simulations. We created our simulated indices of relative biomass (spanning 1970 to 2007 and 1986 to 2007 for the simulated trawl and longline indices, respectively) by multiplying the median yearly biomass estimates by the estimated catchability coefficients for each index. We generated two indices for the trawl index, one that was proportional to biomass, and a hyperdepleted index that had a power curve relationship with a defined shape parameter of β = 2.5. Small amounts of observation error (τ = 0.1) were added to each index for efficient MCMC sampling. We kept the observation error low as we wanted to observe the effects of model misspecification on the parameter estimates and not have the results obscured by noise in the observation process. To aid in comparison between models, the same random seed was used to generate observation noise for the proportional and nonproportional trawl indices.

Results
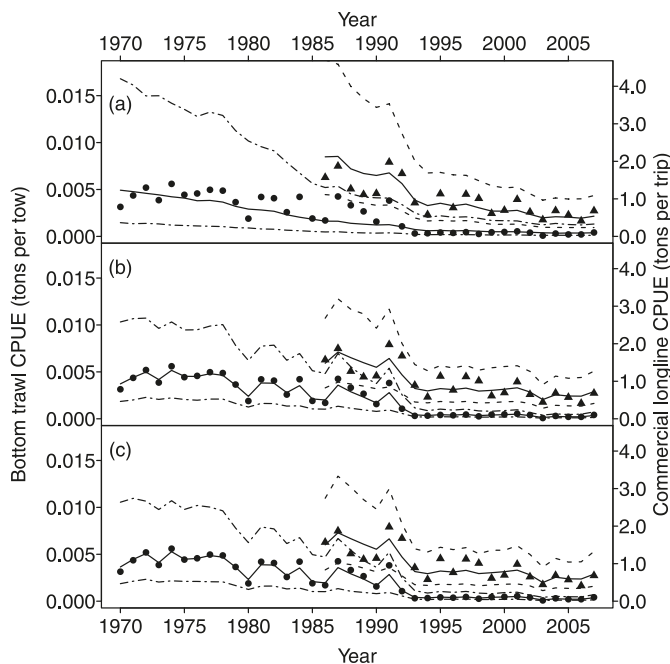
Model summaries and trends

In all four models, posterior distributions for r and K were correlated and had a strong positive skew. Both of these features were expected, as r and K are frequently confounded in a Shaefer model (Haddon 2001) and the positive skew arises from the defined lognormal distribution of the biomass parameter. Regardless, all models passed convergence

Table 2. Summary of data and scenarios used for simulation evaluation.

		Data			
Scenario ID	Model assumptions	$P_{longline}$	P_{trawl}	S_{trawl}	Landings
Model 3	Parameter estimates from Model 3	—	—	—	—
A	Trawl survey assumed proportional		✔		✔
B	Trawl survey assumed proportional			✔	✔
C	Longline index assumed proportional	✔			✔
D	Both indices assumed proportional	✔	✔		✔
E	Both indices assumed proportional	✔		✔	✔
F	Both indices assumed nonproportional	✔		✔	✔
G	Trawl survey assumed nonproportional & longline index assumed proportional	✔		✔	✔

Note: Two simulated trawl indices were created, one that is proportional to biomass (P_{trawl}), and another that is hyperdepleted and follows a power curve ($\beta = 2.5$; S_{trawl}). Both span from 1970 to 2007. The simulated longline series is proportional to biomass and spans 1986 to 2007 ($P_{longline}$).
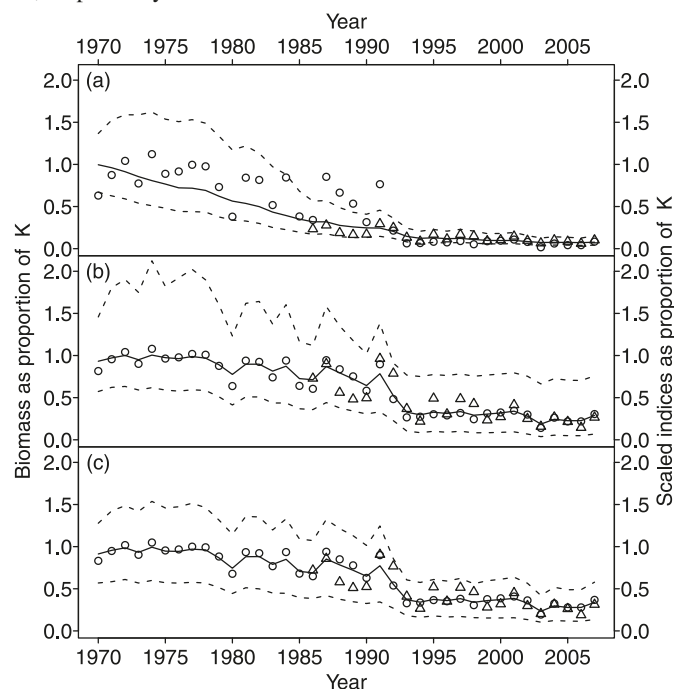
Fig. 4. Surplus production model fits to commercial longline catch-per-unit-effort (filled triangles, ▲) and fishery-independent bottom trawl (filled circles, ●) indices. Panel (*a*) assumes both indices are proportional to biomass (Model 1). Panel (*b*) estimated shape parameters (β_i) in the observation equation for both indices (Model 2). Panel (*c*) is fit of model assuming commercial longline index is proportional to biomass and estimates a shape parameter for the bottom trawl survey (Model 3). Unbroken and broken lines are median and 95% credible limits, respectively.

Fig. 5. Biomass as proportion of carrying capacity (B_t/K) estimates from surplus production model fit to commercial longline catch-per-unit-effort (open triangles, △) and fishery independent (open circles, ○) bottom-trawl indices. Panel (*a*) assumes both indices are proportional to biomass (Model 1); Panel (*b*) Estimated shape parameters (β_i) in the observation equation for both indices (Model 2); Panel (*c*) is fit of model assuming commercial longline index is proportional to biomass and estimates a shape parameter for the bottom trawl survey (Model 3). Observations have been scaled, where appropriate, by the estimated catchability coefficient ($q_{longline}$; q_{trawl}) and shape parameter(s) ($\beta_{longline}$; β_{trawl}) for each index. Unbroken and broken lines are median and 95% credible limits, respectively.

diagnostics. Model 1, in which both indices were defined to be proportional to biomass, did not fit the data well. This is evident by the lack of fit to the trawl index early in the time series and the underfitting during the transition period of high to low biomass in the early 1990s (DIC, –436; Fig. 4*a* and Fig. 5*a*). The model accounted for the lack of fit by estimating a large observation error variance (τ_T^2) for the trawl index (Table 3). Posterior density plots indicated that there was sufficient information to estimate the *r* and *K* parameters (Figs. 6*a* and 6*b*).

Estimating shape parameters for both indices (Model 2) improved the model fit (Fig. 4*b*; DIC, –522). The credible

limits of the biomass estimates contained all of the scaled index values. The credible limits were also substantially wider than in Model 1, owing to the increased uncertainty in *K* (Fig. 5*b*). The median of the posterior for *r*, although slightly smaller, was similar to Model 1 and credible limits were slightly larger. Conversely, the median of the posterior for *K* was slightly larger, but the upper 95% credible limit was almost double that estimated by Model 1 (Table 3).

Table 3. Summary of posterior quantiles of parameters for Models 1, 2 and 3.

Parameter	Model 1			Model 2			Model 3		
	2.5%	Median	97.5%	2.5%	Median	97.5%	2.5%	Median	97.5%
Intrinsic rate of pop. growth (r)	0.015	0.149	0.505	0.007	0.126	0.555	0.007	0.115	0.362
Carrying capacity (K; tons)	24 750	53 270	126 708	20 480	57 225	232 605	24 399	51 580	192 013
Biomass in 1970 (B_{1970}; tons)	22 477	53 670	124 902	14 810	53 900	235 223	18 470	47 430	190 718
Biomass in 2007 (B_{2007}; tons)	1721	4204	10 440	2248	15 565	137 713	5371	16 900	85 271
B_{1970}/K	0.67	1.00	1.37	0.57	0.93	1.46	0.57	0.91	1.28
B_{2007}/K	0.04	0.08	0.15	0.07	0.29	0.76	0.14	0.34	0.58
Longline catchability (q_L)	5.1×10^{-5}	1.3×10^{-4}	3.1×10^{-4}	8.0×10^{-6}	3.6×10^{-5}	1.2×10^{-4}	8.9×10^{-6}	4.2×10^{-5}	1.3×10^{-4}
Trawl catchability (q_T)	3.8×10^{-8}	9.4×10^{-8}	2.3×10^{-7}	1.5×10^{-8}	8.4×10^{-8}	3.6×10^{-7}	1.6×10^{-8}	9.6×10^{-8}	4.0×10^{-7}
Process error variance (σ^2)	0.00	0.02	0.14	0.00	0.04	0.25	0.01	0.03	0.09
Longline Obs. error variance (τ_L^2)	0.02	0.09	0.27	0.03	0.06	0.14	0.03	0.06	0.14
Trawl Obs. error variance (τ_T^2)	0.18	0.32	0.57	0.00	0.09	0.26	0.00	0.08	0.27
Shape parameter for longline	—	—	—	0.35	0.83	3.49	—	—	—
Shape parameter for trawl	—	—	—	1.00	2.06	8.61	1.62	2.48	3.60
Max. surplus prod. (MSP; tons)	340	2005	4012	153	1846	6486	142	1538	5281
Biomass giving MSP (B_{MSP}; tons)	12 380	26 635	63 373	10 240	28 615	116 302	12 200	25 790	96 025
B_{2007}/B_{msp}	0.08	0.15	0.31	0.14	0.58	1.52	0.27	0.68	1.16
DIC		−436			−522			−577	

Observation error for both indices was smaller than Model 1, and the estimated observation error for the trawl index was larger than the longline index. Although there was overlap in the posterior densities of the shape parameters, both were identifiable and the modes of the posterior densities were well separated (Fig. 6*i*). The median estimate for the longline index shape parameter was 0.83; however, about 62% of the probability density of the posterior was less than 1.0, which suggests weak evidence that the index is hyperstable. Conversely, the median estimate for the trawl index shape parameter was 2.06, and 97.5% of the probability density was greater than 1.0 suggesting substantial hyperdepletion in the trawl index. The results from Model 2 suggested that a more parsimonious model, in which a shape parameter is estimated for the trawl index only, would result in a comparable model fit, and indeed Model 3, with one less parameter, had the most support (DIC, –577). Model fit to the observations was similar to Model 2 (Fig. 4*c*); however, yearly biomass estimates had tighter credible limits and still contained all scaled trawl and longline index values (Fig. 5*c*). Estimates of observation error for both indices were virtually identical to Model 2. The range of uncertainty in K was greater compared with Model 1, but less so than Model 2. In contrast, the credible limits of r were much more narrow, yet the median estimate was similar to both Model 1 and 2. The model estimated greater hyperdepletion in the trawl index compared with Model 2, and the posterior of the estimated shape parameter was well defined and had less skew (Fig. 6*n*). We estimate a 59% decline in cusk biomass between 1970 and 2001, a 64% decline from 1970 to 2007, and estimate stock biomass to be at 68% of maximum surplus production under Schaefer model assumptions (MSP, Table 3) in 2007.

Model 4, in which a shape parameter was estimated for the longline index only, had the least support of all shape parameter models (DIC, –497). Severe hyperstability was estimated in the longline index (median, 0.41) and process error was substantially larger than all other shape models (plots not shown).

Model sensitivity

We evaluated the robustness of the model fits and parameter estimates for Models 1 to 3, and further tested Model 3 against alternate forms of the r prior. Omitting the last 7 years of data had little effect on the estimated parameters; however, the predicted observations for both indices were all greater than the omitted data for all models (Fig. 7). Alternate forms of the r prior for Model 3 had relatively little effect on either the model fit or parameter estimates. Indeed, the more informative of the alternate lognormal priors, which had a mean and variance of 1.0, only changed the median posterior estimate of r from 0.115 to 0.122 (95% credible limits of 0.03–0.35), which is very similar to the original Model 3 that had a flat r prior (Table 3). Similar minor changes to the parameter estimates were observed when we replaced the flat priors with informative normal priors with a mean and variance of 1.0 for σ^2, τ_L^2, and τ_T^2. The median estimates for Model 3 became as follows: r, 0.124; K, 48 075; σ^2, 0.036; τ_L^2, 0.064; and τ_T^2, 0.085, which are very close to those estimated when flat priors were used (Table 3).

Fig. 6. Posterior density plots of select model parameters. Where separate parameters are estimated for each data series, the commercial longline catch-per-unit-effort index is described by a grey line and the fishery-independent trawl survey a black line. Priors are identified as broken lines. (*a*) Model 1 (panels *a–d*) assumed both indices were proportional to biomass, (*b*) Model 2 (*e–i*) estimated a shape parameter for both indices; and (*c*) Model 3 (*j–n*) estimated a shape parameter for the trawl survey only.
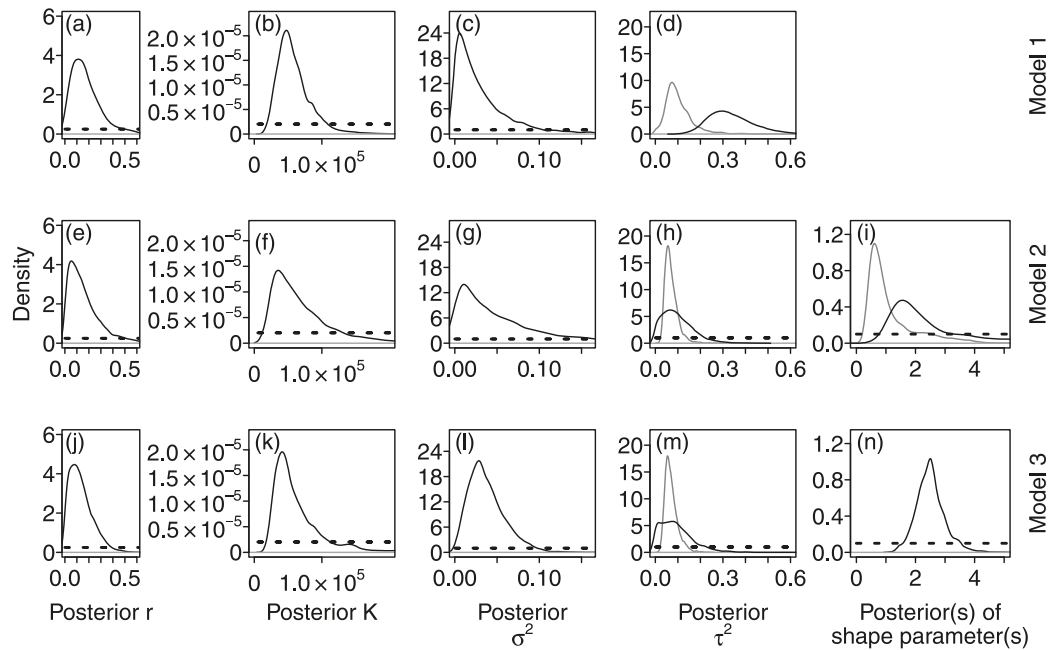
Fig. 7. Standardized residuals of predicted catch rates with the last 7 years of observation data removed. Filled circles (●) indicate years where observation data are present (1970 to 2000) and open circles (○) indicate that no observation data other than fishery removals are included (2000–2007). Panels *a–c* indicate the fishery independent trawl index, and *d–f* indicate the commercial longline catch rate index.
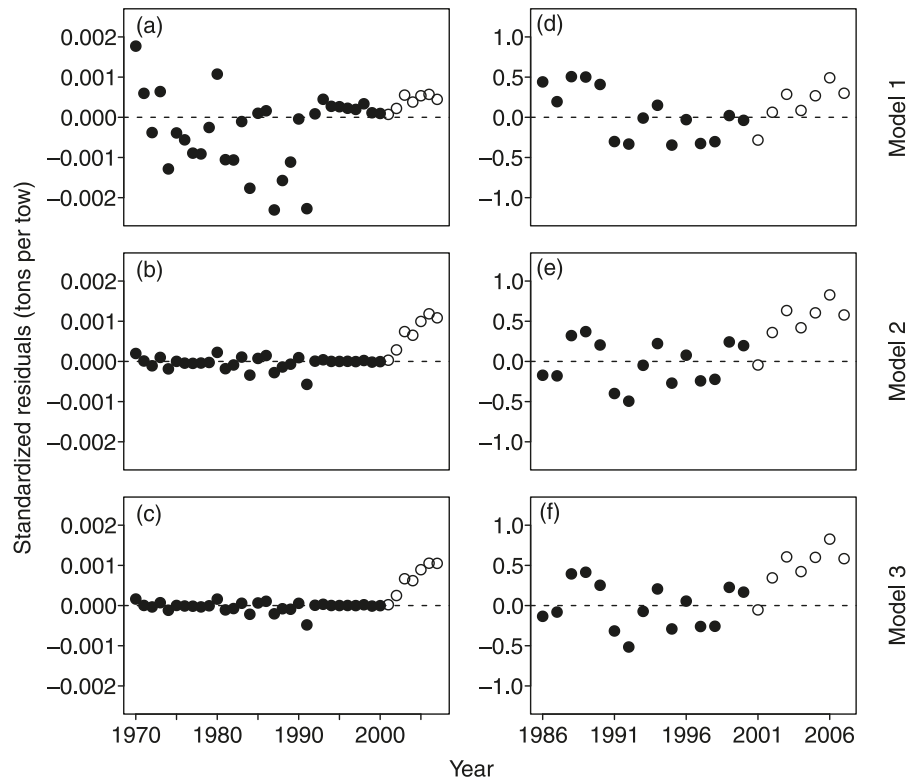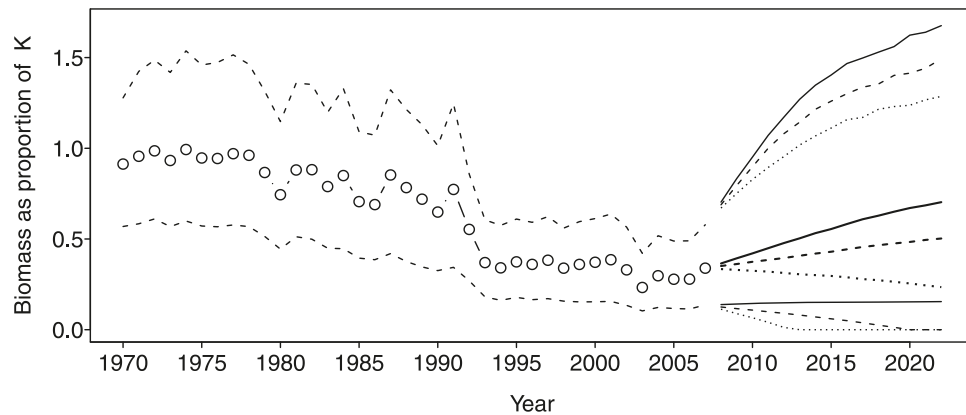

Biomass projections

Population projections using the derived parameter estimates from Model 3 suggest that the current landing limit of 750 t is sustainable and should result in a biomass increase (Fig. 8); however, robustness tests indicate a bias in predicted recovery rates, and the biomass predictions are

Fig. 8. Stochastic projections using Markov Chain Monte Carlo parameter realizations from the surplus production model that estimated a shape parameter for the trawl survey and assumed the longline index to be proportional to biomass (Model 3). Unbroken, dashed, and dotted lines are median and associated 95% credible limits of the biomass estimates corresponding to catch levels of 0, 750, and 1500 tons per year.

likely overly optimistic (Fig. 7). The projection predicts a median biomass increase to 50% of K by the end of the 15-year projection period, which equates to the biomass level that would give MSP under Shaefer model assumptions. In terms of risk, 4% of projected populations went extinct after 15 years at this landings limit. Terminal biomass estimates had wide credible limits, owing to the large uncertainty in the parameter values and stochastic nature of the projections. Indeed, some realizations of the joint posterior distribution for the r parameter were close to zero (3.7% were < 0.01) resulting in very little biomass production during the projection period. A landings limit of 1500 t was clearly unsustainable, with 30% of the simulated populations going extinct after 15 years. Reducing landings to zero resulted in predicted biomass increases to 70% of K after 15 years. An obvious limitation of the projections is that they are based on equilibrium conditions, which do not account for the age-structure of the population or recruitment time-lags. Furthermore, the robustness tests suggest that the models have poor predictive ability and tend to over predict biomass increases.

Simulations

Simulations provided a clearer picture of the benefits of including both indices and the consequences of model misspecification on parameter estimates. Beanplots comparing posteriors of the parameter estimates between Model 3 and the simulated data reveal that model misspecification can cause large biases in initial and terminal biomass estimates, and including both indices improved the precision of parameter estimates (Fig. 9). As with the models in the primary analysis, all models using simulated data had negative mean deviance, pD, and DIC.

The biomass trajectory derived from Model 3 is the basis for all the simulated data scenarios and is the baseline for comparison to all simulations (Table 2). Both posteriors in the Model 3 column are identical, and hence, the beanplots are symmetrical (Fig. 9; Model 3). The parameter estimates for Scenario A show that even when the model assumptions are consistent with the data, a single proportional index spanning the entire time-period (38 years) had insufficient power to fully recapture the parameters of interest (Fig. 9;

scenario A). Scenario B describes the model fit that assumed proportionality to a single 38-year hyperdepleted index and had similarly diffuse posteriors for r, K, and B_0 as scenario A; however, the biomass estimate for 1970 was lower compared with both Model 3 and scenario A (Fig. 9; scenario B). A single proportional index spanning only the last 22 years (Fig. 9; scenario C), akin to only using the longline index and landings data, leads to similarly diffuse parameter estimates as those obtained by only using a single, longer, proportional time series (scenario A). However, the B/K ratios were less biased, compared with scenario A, although median estimates for K and biomass estimates were still biased high, compared with Model 3. This is likely a symptom of both the lack of CPUE data prior to 1986, and possible limitations of the Schaefer process model to fully capture the population dynamics. According to Schaefer model dynamics, the substantial landings prior to 1990 should have resulted in a decline in biomass during this period if the population was starting at carrying capacity. This was not observed in the simulated trawl survey data (which closely resembles the true trawl data; (Fig. 2)). Indeed, although some biomass decline was observed, the trawl survey declines only slightly, far less than should have been observed if the population was following Schaefer dynamics. The lack of observation data in the earlier years allows the model to fully follow Schaefer dynamics earlier in the time series, thus making K and initial biomass larger than what is estimated by the model that used both datasets. Using two indices that were proportional to biomass and modeled as such, allowed us to recapture the parameters of interest (Fig. 9; scenario D); both the posteriors and medians were almost identical to that of Model 3. The median of the posterior for r was slightly lower than the reference model (0.104 compared with 0.115), which is likely due to MCMC noise and (or) the observation error introduced to the simulated indices. In contrast, when the simulated trawl index is hyperdepleted and the shorter index is proportional to biomass, yet we do not account for nonproportionality in the model (scenario E), the posteriors of K and 1970 biomass were almost identical to those of Scenario B, which only used a simulated hyperdepleted trawl index, indicating that

Fig. 9. Select model parameters from simulation models. Beanplots (Kampstra 2008) compare the posteriors of select model parameters from Model 3 (white) to the posteriors from alternate model scenarios (grey posteriors in columns B to G), which use simulated indices of relative biomass derived from the median biomass trajectory estimated from Model 3. The broken horizontal lines are the median of posteriors of select model parameters from Model 3. The bold unbroken horizontal lines are the medians of the posteriors of the alternative model and data scenarios. Rows are estimates of the intrinsic rate of population increase, r, carrying capacity, K, biomass in 1970 and 2007, and the ratio of biomass divided by K. Model assumptions and data used are summarized in Table 2.
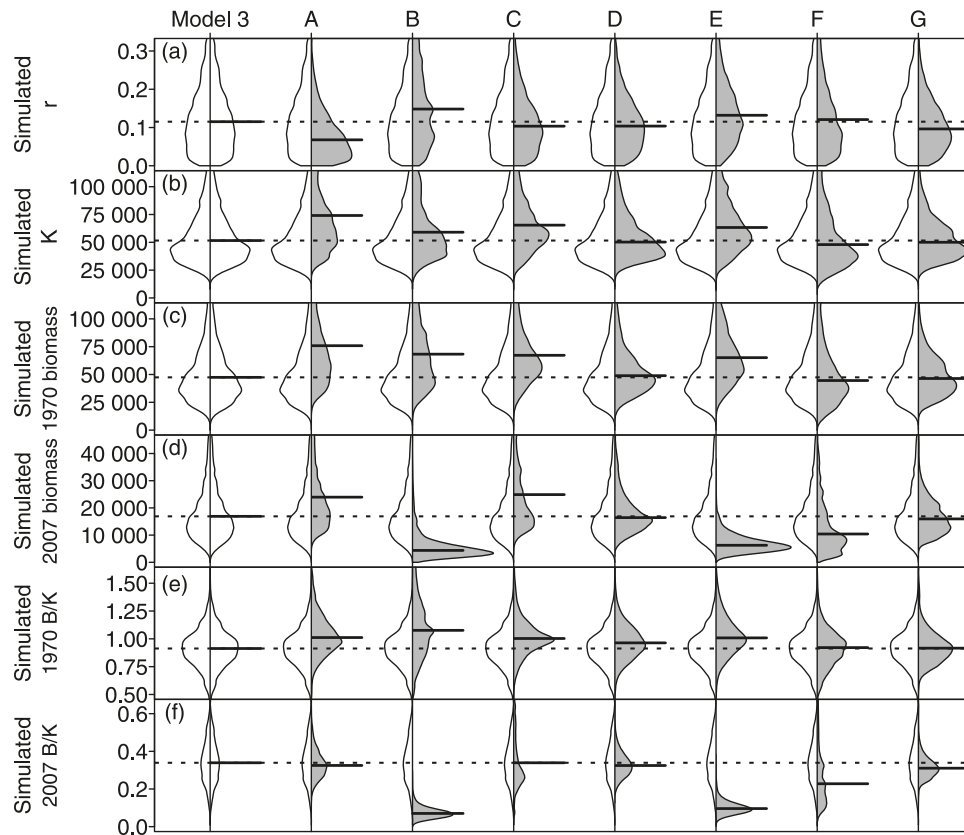
the trawl index is driving the estimates of these two parameters (Fig. 9, scenario E).

Scenario F had the same data characteristics as scenario E, but estimated a shape parameter for both indices. The model was able to obtain better parameters estimates by comparison with scenario E, with the exception of the 2007 biomass estimate, which was approximately 70% of the true value (Fig. 9, scenario F). The medians of the shape parameters were 0.81 (95% credible limits of 0.45–3.65) for the simulated proportional longline index, and 1.99 (95% credible limits of 1.13–8.93) for the simulated hyperdepleted trawl index both of which are very similar to those estimated by Model 2 in our primary analysis (Table 3). Finally, we were able to recapture the parameters of interest when the longer time-series was nonproportional and we included nonproportionality in the model (Fig. 9, scenario G). Similar to Scenario D, which correctly matched the model assumptions to the proportionality of the simulated data, the median of the posterior of r was slightly lower than the reference model. The model was able to estimate the nonproportional shape parameter close to its defined value of 2.5 (median $\beta = 2.44$).

Discussion

By using a Bayesian state-space modeling approach in

WinBUGS, we were able to combine multiple indices in a single population model and identify and accommodate index nonproportionality, thereby improving estimates of cusk population trends and current status. There was weak evidence for nonproportionality of the commercial longline index; however, model fits substantially improved when a shape parameter was estimated in the observation equation of the trawl index, suggesting hyperdepletion of the trawl survey index for cusk. Using Model 3 as a baseline for the "true" biomass trajectory, we determined that including both indices in the model resulted in more precise and unbiased parameter estimates, and yielded better biomass estimates in the terminal and beginning years of the indices. COSEWIC's estimate of decline was primarily based on decline observed in the trawl survey index, and assumed that it was proportional to biomass. Our median estimates of decline of 59% between 1970 and 2001, and a 64% decline from 1970 to 2007, while still substantial, are much less severe than the 93% decline from 1970 to 2001 estimated in the COSEWIC assessment that used the raw index data (COSEWIC 2003). However, because our biomass estimates are smoothed by the model, and determining percent declines from raw index data can be unreliable, to make the estimates of decline of the two analyses more comparable we ran the model using only the survey data and estimated a median 89% decline from 1970 to 2001, assuming the

index was proportional to biomass. Use of the longline index alone, also leads to overestimates of cusk decline: a decline of 81% from 1970 to 2007, and 63% from 1986 to 2007 compared with 52% for this time period when both indices are used and nonproportionality of the survey index is included in the model (i.e., Model 3). Our lower estimate of decline will likely not have an impact on the COSEWIC designated status for cusk. Although the estimated decline is less severe, new aging analyses, although preliminary, suggest that generation time is approximately 15 years, rather than 9, as cited in the COSEWIC report (COSEWIC 2003). A decline of 64% in 2.5 generations is sufficient to warrant "threatened" status under the COSEWIC guidelines (COSEWIC 2009). Accounting for nonproportionality can substantially improve estimates of population trends; however, our simulations highlight that caution needs to be applied when using estimates of index nonproportionality from other analyses. For example, in Scenario F of our simulations, 70% of the probability density of the estimated shape parameter for the simulated longline index was less than 1.0 (median 0.81), even though the index was simulated to be directly proportional to biomass. This is an indication that there is confounding in the estimation of multiple shape parameters and thus using shape parameter estimates as informative priors in other analyses could lead to biased biomass trajectories. Furthermore, in our primary analysis, Model 4 had a median shape parameter estimate 0.41 and had more DIC support compared to Model 1 that assumed both indices were proportional to biomass. This estimate of hyperstability is far more severe than those estimated for directed commercial fisheries (Harley et al. 2001) and is therefore unlikely for a bycatch species such as cusk. Therefore, when specifying a model with shape parameter(s), it is important to consider whether there is an a priori reason to expect nonproportionality in the indices.

Our simulation models also show that including multiple indices substantially increases the power to recapture parameter estimates when nonproportionality is accounted for in the model when, and if, present in the data. We also discovered that DIC alone may not be a reliable metric for some Bayesian state-space model applications. An additional model we preliminarily tested, but is not described in the manuscript, was to test for a knife-edge change in catchability in the trawl survey in 1992 when the survey trawl index rapidly declined. According to DIC, this model had the most support using both the real and the simulated data, even though in the latter case we specified that a change in catchability was not responsible for the declines. This underscores the importance of using simulated data to investigate further the plausibility of the models.

We have shown that simply assuming the trawl survey index to be proportional to biomass can result in incorrect estimates of population change. This is of concern because this trawl survey is being used increasingly for population assessments of bycatch species, because it is frequently the only source of long-term fishery-independent time-series data on the east coast of Canada. Nonproportionality may be an issue for any species whose distribution is not well represented in the trawl survey design. While it maybe tempting to discard indices that have questionable proportionality relationships, in favor of other time-series data

with known relationships to population biomass, this approach is unsatisfactory for a number of reasons. First, the index to biomass relationship is poorly known for most bycatch species and choosing one index over another will likely be ad hoc. Second, the potentially nonproportional index may be the longest time-series available and other indices may have little contrast and only begin after population declines have already occurred. Discarding long time-series has the potential to create shifting baselines (Pauly 1995) where current estimates of population status are viewed from a recent perspective. This can lead to underestimates of population decline (Rosenberg et al. 2005). Even with the inclusion of these relatively long time-series data, a lack of baseline data will still be a challenge because they began on the east coast of Canada in 1970, which is well after large scale industrial fishing began.

Although we were limited to using broad flat priors in this analysis, the Bayesian approach allows for ancillary information to be incorporated through the priors to reduce uncertainty in the parameter and biomass estimates and hence is particularly useful for data-poor species (Chaloupka and Balazs 2007; Swain et al. 2009). For example, demographic methods can be used to construct a prior for r (McAllister et al. 2001). We abandoned efforts to develop an informative r prior as the dearth of life history data and current uncertainty in aging would have resulted in a highly diffuse and bi-modal prior that would have added little to the analysis. Indeed, preliminary radio-carbon bomb calibration of cusk otoliths suggest that 95% of cusk are mature by 15 years and maximum age may be over 40 (P. Comeau, Marine Fish Division, Bedford Institute of Oceanography, Fisheries and Oceans Canada, Daertmouth, N.S., personal communication 2008), which is twice that of earlier estimates (COSEWIC 2003). Developing a credible prior for carrying capacity is also problematic as the true historical biomass of cusk before the onset of fishing will never be known with much precision. However, a joint posterior probability plot (not shown) of the r and K parameters indicate substantial confounding between the two. Although this can cause problems for parameter estimation, it also means an informative prior on r also provides information for the K parameter as well (McAllister et al. 2001).

The stochastic projections suggest that the current landing limit of 750 t should be sufficient to increase population biomass. However, the retrospective analysis we conducted by removing the last 7 years of data indicate that biomass should have increased over the last seven years but this has not been observed. This suggests that our projections have limited value for determining if biomass increases should be expected at the current landing limit and calls into question the utility of our parameter estimates for predicting population recovery. The lack of recovery may be due to a number of factors. First, landing limits may be ineffective because of high bycatch mortality. Although landing limits were designed to reduce fishery induced mortality, they may be ineffective because, as a relatively deep water species, cusk may suffer substantial barotrauma when captured. There are no estimates of bycatch mortality in the longline fishery, but estimates in the lobster fishery, which operates at similar depths, are >50% (DFO 2008). In our analyses, we equated landings with fishery removals and therefore we almost cer-

424

Can. J. Fish. Aquat. Sci. Vol. 68, 2011

tainly underestimated true fishing mortality after 1999 when the first landings limit was implemented. Second, the Schaefer model does not include age-structure or recruitment time lags, and therefore our projections may exaggerate the predicted recovery rate. Evidence that time lags may be important can be seen in Fig. 2 where substantial biomass was removed in the early 1970s without a concurrent decline in the trawl survey index. Also, the symmetrical biomass production relationship of the Schaefer model may be unrealistic if age structure has a strong influence on the population production rate (Maunder 2003). Third, abnormally poor recruitment between 2000 and 2007 could also explain the lack of recovery. Alternatively, a regime change of reduced productivity or increased natural mortality in the latter period of the time series would result in a decrease population growth rate and be consistent with our poor model predictions. We attempted to model this by estimating separate r parameters before and after, the mid-1990s, but model fits did not improve, nor did the predictive ability of the model. Unfortunately, there are limited data to test these hypotheses.

In conclusion, our analysis suggests that the cusk fishery-independent trawl survey index suffers from hyperdepletion, which, if not accounted for, results in exaggerated estimates of population decline. The high levels of uncertainty in our parameter estimates are a result of the limited data available, as well as the low contrast and "one-way trip" trends in both catch rate indices. High levels of uncertainty in population parameters and historical biomass levels are characteristic of many bycatch species and management strategies that include these levels of uncertainty need to be employed. Managers also may seek to increase monitoring to achieve greater certainty in parameter estimates, and hence greater management control of this species. The effectiveness of the current landings limit to aid population recovery is uncertain as our robustness tests suggest that the population should be recovering, but monitoring data suggest that it is not. Further research is needed to estimate bycatch rates in the longline fishery to determine whether a landings limit is an effective management strategy for cusk recovery. In addition, further aging and age validation research is needed so that more realistic models, for example, that include time lags in recruitment can be used (e.g., Meyer and Millar 1999a; Millar and Meyer 2000). Although we were unable to include life-history information through the use of informative priors, the Bayesian approach is promising for the assessment of poorly monitored species where data is limited and time series have little information on population parameters.

Acknowledgments

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