Prerecruit survival and recruitment of northern Gulf of St Lawrence Atlantic cod

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Recruitment (R) of exploited marine fish populations is usually modelled exclusively as a function of spawning-stock biomass (SSB). A problem arising when modelling over long time-series is that the nature of the R–SSB relationship is unlikely to be stationary. Changes are often interpreted as productivity regime shifts and are linked to alterations in prerecruit survival rate. We examine the role of environment and predation by fish and harp seals as factors affecting the R–SSB relationship in the northern Gulf of St Lawrence cod, by fitting linear models using combinations of covariates to explain cod prerecruit survival. The most parsimonious model (based on a Bayesian Information Criterion, BIC) included cod, mackerel, and temperature, whereas redfish and seals did not appear in any of the best-fit models. Recruitment models derived from this analysis could be used in operating models for management strategy evaluation simulations for northern Gulf cod, so one could develop harvest control rules that are robust to changes in recruitment productivity regimes.

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Introduction

Recruitment (R) is usually modelled exclusively as a function of spawning-stock biomass (SSB; Cushing, 1973; Garrod and Jones, 1974; Csirke, 1980). This is advantageous in fisheries projection modelling because R and SSB are intrinsic to the population and therefore can be projected without recourse to external information. R is generally positively linked with SSB, but the exact nature of the relationship varies widely by stock and species (Myers and Barrowman, 1996). Additionally, R–SSB parameter space is often characterized by rapid changes in productivity regime where the R–SSB relationship holding during a given period appears to shift to a new stable state (Chen, 2001; Beamish et al., 2004). This implies that R forecasts are less certain with distance from the terminal data year and that setting management reference points assuming that the R–SSB relationship is stationary may not be valid. The failure to consider influences other than SSB on R may therefore be conceptually inaccurate and result in serious management errors (Beamish et al., 2004). This is especially true for management strategies that rely on long-term projections and appropriate characterization of uncertainty about these projections.

Many environmental factors, such as temperature, salinity, and oxygen conditions can induce changes in productivity (Lees et al., 2006). Productivity regime shifts are usually identified in fisheries as changes in the rate of recruitment (recruitment to a fishery divided by the SSB), implying that these factors affect mortality in the prerecruit stages. Predation is often described as the main determinant of prerecruit survival, but any environmental factor that influences survival from hatching to the end of the prerecruit stage will affect the R–SSB relationship. In the late 1990s, the assessment group for the northern Gulf of St Lawrence Atlantic cod (Gadus morhua) stock adopted a retrospective change in natural mortality (M) from 1986 on (DFO, 2007), where M was doubled from 0.2 to 0.4 because it appeared that many conditions changed then (Savenkoff et al., 2006). This shift corresponded to the start of the rapid decline of the stock, which crashed and was placed under moratorium from 1994 to 1996 and again for 2003. No clear mechanism has been proposed for this change in M, which was necessary to reconcile catches with estimates of population size, but the implication for a cohort reconstruction model is that recruitment rate changes.

Predation is an important source of mortality of young cod in the northern Gulf of St Lawrence. For instance, it was estimated to represent 71% and 95% of total mortality in the mid-1980s and mid-1990s, respectively (Savenkoff et al., 2006). Prerecruit cod face a diverse predator assemblage: a large harp seal (Phoca groenlandica) population resides in the Gulf for ~6 months of the year and tends to concentrate prey consumption in the north, which may impact juvenile survival at certain times of the year (Hammill and Stenson, 2000). Pelagic fish may also inflict significant predation mortality on larval and early juvenile cod. It is considered that about one-third of the Atlantic mackerel (Scomber scombrus) stock spawning in the southern Gulf migrates to the northern Gulf to feed from July to October (Savenkoff et al., 2005). Two stocks of Atlantic herring (Clupea harengus) are also found in the northern Gulf, and the intense feeding period of

the spring-spawning stock spatially and temporally overlaps with cod spawning and larval development (Moores and Winters, 1984; McQuinn and Lefebvre, 1995; Ouellet *et al.*, 1997; Méthot *et al.*, 2005). Redfish (*Sebastes* spp.) were also considered a major predator on small cod in the 1980s and early 1990s when redfish were abundant, but thereafter their importance as a cod predator decreased (Savenkoff *et al.*, 2005). Finally, juvenile cod are cannibalized by adults, which were considered the main predators of juvenile cod when cod dominated the ecosystem during the late 1970s and early 1980s (Savenkoff *et al.*, 2006). Prerecruit stages of the northern Gulf cod could therefore undergo several survival bottlenecks as they grow into the preferred prey size windows of their various predators.

The objective of the present study was to discern the role of predation and environment on prerecruit survival of Atlantic cod in the northern Gulf of St Lawrence through external factors impacting the R–SSB relationship. We focused on the abundance and food consumption of the main predators (fish and seals) in the system as determinants of young (<500 g) cod mortality, and we used mean temperature in the cold intermediate layer (CIL; 30–100-m water depth) as an environmental descriptor. We also used the adult cod condition factor itself as an integrated descriptor of environmental conditions (Dutil and Lambert, 2000). Following Swain *et al.* (2000) in a study on the southern Gulf cod, we fitted linear models with combinations of covariates to explain prerecruit survival.

Material and methods
Data
Cohort model reconstructions of the northern Gulf cod stock were first considered as the source for R and SSB data. However, regression model fittings were critically sensitive to decisions on the rate of natural mortality (M) used in the stock assessment. M is not well understood for this stock and is currently under review after important changes in recent assessments. Although M is a scaling variable and a change in its value for the whole time-series would not affect the stock trend, M changes value within the assessment time-series, and this affects the R/SSB ratio between periods. To remove the influence of choosing a value of M for the assessment model that is not well defined, R and SSB time-series were derived from the northern Gulf stratified random sampling trawl survey (Doubleday, 1981), which has been conducted annually since 1984. The survey changed vessel and gear in 1990 and again in 2006, but the series was corrected for size-based catchability using comparative tows to obtain a consistent series until 2007 (Savenkoff *et al.*, 2004). New recruits were considered to be fish aged 3 years, corresponding to the size interval of 34–44 cm in the survey from 1987 on. The SSB index was defined as the biomass of cod ≥ 7 years old (7+), corresponding to a size of ≥ 54 cm. The assessment of the northern Gulf stock shows that biomass of 7+ cod strongly correlates with SSB and therefore captures the trends in mature fish biomass for the purposes of this study.

Herring abundance was taken from the last cohort model assessment (1984–2004) conducted on the spring- and autumn-spawning herring stocks in the northern Gulf (4R; DFO, 2004). Herring were assumed to have an average length of 15 cm and all biomass was ascribed to that length. Mackerel feeding in the northern Gulf during summer represent about one-third of the southern Gulf spawning subpopulation (Savenkoff *et al.*, 2005).

The southern Gulf mackerel represents about half of the Northwest Atlantic population, which overwinters off New England and is assessed each year by the National Marine Fisheries Service (NMFS). Information on mackerel abundance was provided by the most recent assessment for this stock (NEFSC, 2006). The average size of mackerel in the stock was estimated from the NMFS winter survey, and all biomass ascribed to this weight category was converted to length using length–weight (L–W) regressions found in www.fishbase.org, i.e. $L = 0.0038\,W^{3.2}$, where W is in kilogrammes and L is in centimetres. This length varied between 6 and 43 cm. Abundance-at-age of harp seals was taken from Hammill and Stenson (2005). This dataset (1960–2004) is a reconstruction of seal abundance using overflight surveys and accounting for hunting and pupping rates. Cod and redfish abundance data were taken from the DFO northern Gulf summer survey and corrected for size-dependent gear selectivity and catchability for changes in gear.

The temperature signal used to characterize the conditions relevant to cod recruitment was the average annual temperature in the CIL between 30 and 100 m deep (Galbraith *et al.*, 2007). Although this temperature may not reflect the water layer in which young cod live, the CIL temperature and thickness is known to be an important summary indicator of environmental conditions in the northern Gulf of St Lawrence (Galbraith *et al.*, 2007). Therefore, we assume that it should also influence cod recruitment directly or indirectly. As another summary indicator of environmental conditions and how it affects cod specifically, we examined the influence of cod condition factor as a summary of external influences on cod. Condition factor was measured as the August condition from the DFO survey for cod aged 5–10 using the Fulton somatic index (K). The condition factor is considered here to be a result of cod feeding, which has been shown to be a function of environmental conditions (Dutil and Lambert, 2000).

Calculating predation risk
Predation risk for prerecruit cod was calculated by modelling a predation size spectrum (PSS) for cod (cannibalism), redfish, mackerel, herring, and seals (Duplisea, 2005). To calculate a PSS, the lognormal predator/prey body weight ratio (PPR) was modelled by predator species and aggregated to make the PSS. PPR was set to 250 for cod (Scharf *et al.*, 2000), 1000 for redfish, 3500 for mackerel, 10 000 for herring (Darbyson *et al.*, 2003), and 5000 for harp seals (Chassot *et al.*, in press). Then, an energy demand (ration) was calculated considering the size of the different predators. Energy demand was allocated over the prey size range determined from the distribution of PPR for each predator size, and scaled by the relative abundance of each predator size. This resulted in species-specific predation spectra, which were summed to achieve the PSS.

Predation risk of prerecruit cod was then derived by taking the PSS predation on age 0 cod in year t and on age 1 cod in year $t+1$, etc. Size-at-age groups were determined considering a size at recruitment (age 3) of 500 g. Size at younger ages was determined by fitting a von Bertalanffy growth curve cast in terms of weight for a M_∞ (maximum size) of 25 kg and growth rate of 0.5 year^{-1}. This calculation yields a quasi-linear size-at-age curve between hatching and recruitment, and although the present method is technically more accurate, a linear interpolation gives essentially the same results for cod recruiting at age 3. Predation risk differs from the

actual predation because it represents the extent of mortality predators would have inflicted on a particular prey size (or size range) if they systematically met their ration and fed according to the lognormally distributed prey-size preference.

The forcing ascribed to predation risk and used as variables in the linear model is simply statistical and in reality, the model cannot differentiate competition from predation. We have attempted to focus the statistics more directly on predation effects by taking predation risk indices derived from the PSS, although predation risk is largely driven by predator biomass.

Model fitting

Linear models were fitted using the BICREG function (Raftery *et al.*, 1997) in the BMA library in the statistical software R. BICREG uses a Bayesian Information Criterion (BIC) to select a parsimonious set of models, and produces an average model with variable coefficients weighted by the posterior probability of component models. BICREG generates a model with better predictive capability than any single component model, but the procedure was used here principally to rank models based on parsimony. What results is a single or series of independent variables that explain some of the variance in prerecruit survival (e.g. Swain *et al.*, 2000):

$$\log(R/\text{SSB}) = k + a \log(\text{cod}) + b \log(\text{redfish}) + c \log(\text{herring})$$
$$+ d \log(\text{mackerel}) + e \log(\text{seal})$$
$$+ f \log(\text{temperature anomaly} + 1)$$
$$+ g \log(\text{condition}).$$

The BICREG procedure drops variables in and out of the linear model by changing their coefficients from 0. Occam's window (Raftery *et al.*, 1997), which specifies that models are not allowed to contribute to the average if they contain a more probable submodel, was used in model selection. This procedure essentially eliminates redundancy in the final set of models.

One way to fit a standard Ricker stock–recruitment curve is to fit a linear model of (R/SSB) against log(SSB), so the descending limb of the relationship is some sort of self interference (intraspecific competition or cannibalism). This method of fitting the Ricker model can produce biased coefficients and spurious relationships. We did not include SSB as a predictor of R/SSB for these reasons and because we were most interested in the affect of external variables on cod prerecruit survival. Residuals of all the fitted models were examined for autocorrelation. None of the models fitted to cod recruits log(R/SSB) showed any significant autocorrelation.

Results

The cod prerecruit survival index R/SSB usually decreased as a function of predation risk, although it was neither linear nor consistently negative (Figure 1, Table 1). The strongest relationship with a predation risk variable was with cod itself (i.e. cannibalism), and weaker relationships were found for redfish, mackerel, and herring, and survival rate actually appeared to increase at the time of high risk of harp-seal predation (Figure 1, Table 1). R_3/SSB was negatively related to cod condition, and weakly related to positive temperature anomaly (Table 1). Of the 13 possible correlations between survival and other variables, six were significant (Table 1).

The BICREG variable-selection procedure for linear models produced five models, two with three variables, two with two variables, and one with one variable (Table 2). No single variable appeared in all models, so no variable had a probability of a non-zero coefficient equal to 1. Cod predation risk was the most likely variable to appear in a model, whereas redfish and seals did not appear in any model. Although mackerel predation risk had neither a strong nor a significant correlation with R_3/SSB (Table 1), it did appear in three of the five models describing survival, but never alone. Temperature anomaly was the important environment variable and appeared in three of the five most parsimonious models.

All models fitting R/SSB provided similar estimates, and no major departure from the average model was observed (Figure 2). No single model explained >54% of the variance in data (Table 2). The fifth model contained only the environmental variables condition and temperature anomaly, and this model differed most from the average model. It would have predicted better prerecruit survival around the year 2000 and poorer survival in more recent years, but it had an r^2 of just 0.31, so one cannot place much confidence in its predictions.

A sensitivity analysis was undertaken to show the influence of PPR on the probability of inclusion of an explanatory variable in the average model. The PPR value for all predators except cod had only a minor influence on the probability of variable inclusion in a model (Figure 3). Most of the changes were for smaller PPR ratios (i.e. predator and prey are closer together in size). Cod PPR in the range 300–400 (i.e. a cod predator is 300–400 times larger than its cod prey by weight) showed some relatively large differences in probability of variable inclusion in a model. In that PPR range, cod and mackerel predation risk and temperature anomaly were less likely to be included in a model, and herring predation risk and condition factor were slightly more likely to be included. When cod PPR increased above 400, cod predation risk and temperature anomaly regained a similar probability of inclusion in the model, but the probability of mackerel predation risk continued to decline, and condition factor essentially took its place. The sensitivity analysis suggests that for certain intervals in cod PPR, there may be changes in model structure describing recruitment rate, but for most cod PPR values (using means and ranges in Scharf *et al.* [2000]), we calculated that some 4% of PPR values would fall in the size range 300–400), indicating that cod has a similar probability of inclusion in a model.

Discussion

Traditionally, fisheries science has modelled recruitment purely as a function of SSB and has considered intraspecific competition as the reason *R*–SSB curves are not linear (Cushing, 1973; Garrod and Jones, 1974). Fish usually live in multispecies communities or assemblages, making interspecific competition and predation particularly important factors to consider in the assessment of single-species recruitment (ICES, 1999), in addition to intraspecific factors. On top on these biological interactions, environmental conditions will affect prerecruit survival (Planque and Frédou, 1999). Therefore, some studies have attempted to include abundance of other species (ICES, 1999; Swain and Sinclair, 2000; Swain *et al.*, 2000), temperature (Begg and Marteinsdottir, 2002; Fiksen and Slotte, 2002; Marjomäki, 2004), coastal currents (Begg and Marteinsdottir, 2002), windforcing during larval life (Marjomäki, 2004), and plankton abundance (Begg and Marteinsdottir, 2002) in the calculation for recruitment of

Figure 1. Prerecruit survival (R/SSB) for northern Gulf of St Lawrence cod plotted against various environment and predation variables. Predation risk is a modelled value representing the potential predation inflicted by that species on prerecruit cod sizes. Predation risk values are comparable within plots, but not between them. The temperature anomaly and cod condition were averaged over the three prerecruit years as composite environmental indicators. Lines are spline smooths (d.f. = 4) through the annual points.

Table 1. Spearman correlation coefficients between variables.

	Cod	Herring	K_2	K_3	Mackerel	R_2	R_2/SSB	R_3	R_3/SSB	Redfish	Seal	SSB	TA_2
Herring	**0.78**												
K_2	**0.74**	**0.45**											
K_3	**0.53**	**0.28**	**0.87**										
Mackerel	−0.26	−0.51	0.13	0.16									
R_2	**0.80**	**0.66**	**0.80**	**0.56**	−0.20								
R_2/SSB	**−0.40**	−0.38	−0.29	−0.41	−0.01	−0.03							
R_3	**0.53**	0.38	**0.57**	**0.65**	−0.29	**0.52**	−0.29						
R_3/SSB	**−0.60**	**−0.50**	**−0.46**	−0.24	−0.07	**−0.48**	**0.53**	0.11					
Redfish	**0.54**	0.27	**0.57**	0.40	−0.13	**0.61**	0.12	0.25	−0.28				
Seal	**−0.60**	**−0.80**	−0.26	−0.15	**0.81**	**−0.57**	0.14	**−0.51**	0.20	−0.40			
SSB	**0.80**	**0.75**	**0.76**	**0.66**	−0.15	**0.74**	**−0.65**	**0.58**	**−0.67**	0.31	−0.53		
TA_2	**0.64**	0.27	**0.74**	**0.64**	0.19	**0.60**	−0.16	**0.53**	−0.19	0.37	−0.14	**0.51**	
TA_3	**0.44**	0.11	**0.70**	**0.82**	0.26	0.40	−0.30	**0.47**	−0.11	0.38	0.01	0.43	**0.84**

Cod, Herring, Mackerel, Seal, and Redfish refer to the predation risk on prerecruit cod inflicted by these groups, SSB is the biomass of cod ≥ 54 cm, and R_a/SSB is the prerecruit survival rate measured as the number of recruited cod (age 2, 22–34 cm; age 3, 34–42 cm) divided by the SSB (biomass of cod 54+ cm 2–3 years earlier). R_a is the number of recruits at age a lagged by a years relative to SSB. K_a is the mean condition factor of cod aged 5–10 in the a prerecruit years corresponding to the R_a prerecruit period. TA_a is the mean temperature anomaly in the 30–100-m water layer in the a prerecruit years corresponding to the R_a prerecruit period. Emboldened values are significant at a level of $p < 0.05$.

Table 2. Regression model fits of variables to cod survival rate (R/S) where cod recruit at age 3, using Bayesian model averaging (BICREG).

Variable	Model 1	Model 2	Model 3	Model 4	Model 5	Average	$p \neq 0$
Intercept	−2.915	−2.267	−3.819	−3.404	−2.464	−2.771	1.00
Cod	−1.095	−0.828	–	–	–	−0.848	0.85
Mackerel	−0.589	–	−1.055	−0.738	–	−0.415	0.64
Temperature anomaly	1.312	–	1.205	–	2.673	0.868	0.63
Herring	–	–	−2.452	−1.978	–	−0.251	0.11
Condition factor	–	–	–	–	−13.287	−0.473	0.04
Redfish	–	–	–	–	–	0.000	0.00
Seal	–	–	–	–	–	0.000	0.00
r^2	0.54	0.35	0.44	0.33	0.31	–	–
BIC	−6.71	−5.72	−2.50	−1.86	−1.31	–	–
Posterior probability	0.53	0.32	0.06	0.05	0.04	–	–

Models 1–5 are the coefficients of the five best models meeting Occam's window criterion; average is the Bayesian modelled average coefficient of the models; $p \neq 0$ is the probability that a variable is not equal to 0 in the average model; r^2 is the coefficient of determination; the posterior probability is the probability associated with an individual model. Posterior probability is a negative exponential function of the BIC value.
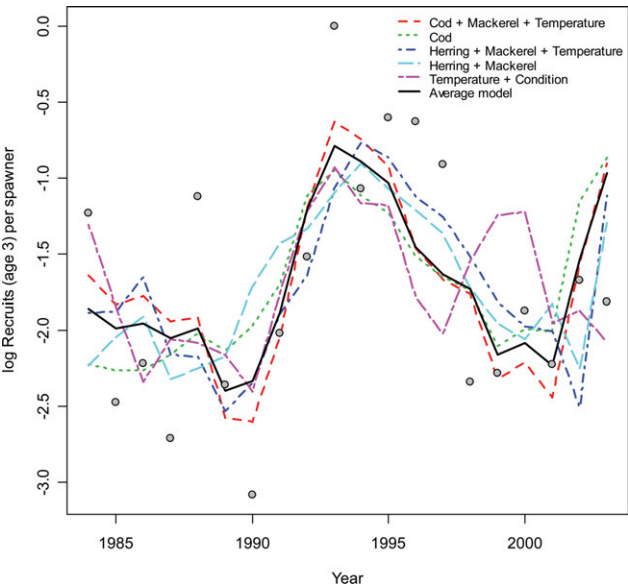

Figure 2. Prediction of northern Gulf cod prerecruit survival using the top three regression models, the average of these models, and the standard Ricker model. Prerecruit survival is the number of age 3 cod from the summer scientific survey lagged by 3 years divided by the biomass of spawning-sized cod in the survey, standardized by the largest value in the series. Points (as year) are the survey data.

a particular stock. Swain *et al.* (2000) performed the exercise of fitting multiple models to prerecruit survival for the southern Gulf of St Lawrence cod. They used environmental variables as well as seal abundance and the biomass of predatory pelagic fish, which were hypothesized to prey on prerecruit cod. Their results highlighted a strong negative relationship between cod R/SSB, and the biomass of small pelagic fish (Atlantic mackerel and Atlantic herring). This link provided an explanation for the lack of a recovery of this stock following the crash of the early 1990s (the period of great abundance of pelagic fish), in contrast to the relatively quick recovery after a first collapse in the 1970s (the period of low abundance of pelagic fish), whereas fishing effort was strongly curtailed during both periods.

Following Swain *et al.* (2000), we attempted to explain better the recruitment dynamics of the northern Gulf cod stock using

indices of predation risk inflicted on prerecruits from fish and harp seal predators and two environmental variables. The exercise showed that the most parsimonious model explaining prerecruit survival contained cod cannibalism, mackerel predation, and the temperature anomaly. Models fitting the survival rate of cod in the first 3 years of life showed that cod cannibalism was the most critical explanatory variable, and that mackerel predation and temperature anomaly were somewhat less important, though still significant. All variables except redfish and harp seals made some contribution to explaining prerecruit survival.

Surprisingly, we found only a weak relationship between cod prerecruit survival rate and predation risk from herring. This contrasts with the southern Gulf cod, whose prerecruit survival was strongly related to small pelagic fish abundance (Swain and Sinclair, 2000). The overlap between herring and early stages of cod also depressed survival to the juvenile stage in the North Sea (Daan, 1980) and the Baltic Sea (Köster and Möllmann, 2000). Despite indications that herring stocks overlap with northern Gulf cod eggs and larvae on the west coast of Newfoundland (Moores and Winters, 1984; McQuinn and Lefebvre, 1995; Ouellet *et al.*, 1997; Méthot *et al.*, 2005), we found little evidence of a predation mortality effect attributable to herring in the prerecruit period.

Our study is essentially an examination of recruitment model uncertainty. Rather than using just a standard Ricker or Beverton–Holt recruitment model, we allowed many variables to influence the rate of recruitment. It is of course interesting to know which variables appear to be the most important descriptors of recruitment rate, but it is useful also to discover how variables act in concert to affect realized recruitment. For example, if one examined mackerel potential predation on juvenile cod as a descriptor of cod prerecruit survival, one might discount it in a single variable study because it is only weakly and insignificantly correlated with cod survival. If, however, one includes temperature anomaly and cod cannibalism risk as other variables in the recruitment model, mackerel predation risk gains prominence as a useful descriptor of recruitment rate. This results because the descriptor variables themselves are not independent. Swain *et al.* (2000) reached a similar conclusion and speculated that a trophic triangle exists between seals, pelagic fish, and cod, where more seals may actually improve the rate of cod recruitment by preying on herring. This type of trophic triangle is not uncommon in multispecies analyses
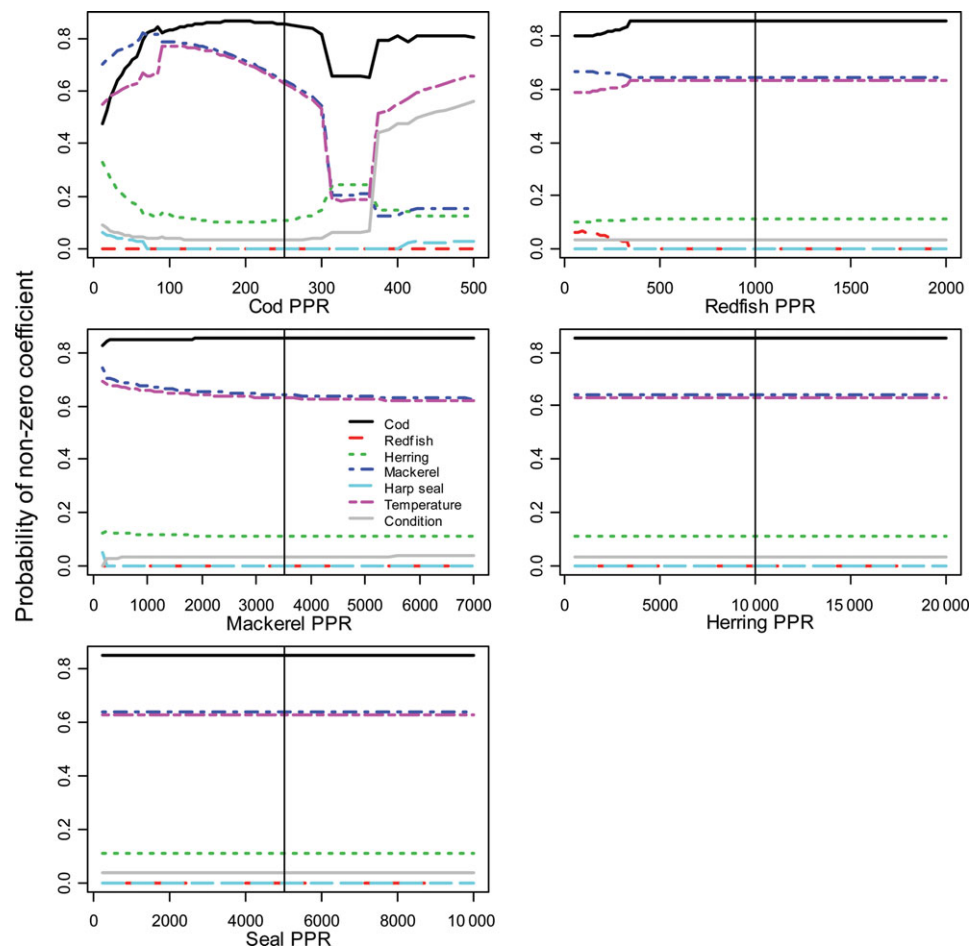
Figure 3. Sensitivity of model variable selection to changes in the predator/prey size ratio of the four predators considered. A non-zero coefficient in the linear model describing R/SSB indicates the inclusion of that variable in the model. Cod, herring, mackerel, redfish, and seal indicate the potential predation risk inflicted by these predators on prerecruit cod. The *status quo* PPR is depicted by a vertical line on each plot. PPR values up to $100 \times$ *status quo* were considered, but had practically no influence on variable selection, so are not shown here.

(Jennings *et al.*, 2001; Yodzis, 2001) and serves as a warning, assuming simple variable-on-variable cause-and-effect relationships. It is also of note that for the same reasons, one can and should find counter-intuitive sign changes in the fitted coefficients for a variable. In this way, one can view the foodweb and could expect signs of fitted coefficients to be revealed in a qualitative signed di-graph analysis (Dambacher *et al.*, 2003).

The northern Gulf cod stock (Laurentian North) is considered "threatened" by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC), and was recommended for listing under Canada's Species at Risk Act (SARA). A "threatened" designation under SARA compels the responsible government body to develop a recovery plan for the stock, which would consist of modelled population trajectories in the face of uncertainties in recruitment and mortality rates. Although the Minister of Fisheries and Oceans Canada declined to list the northern Gulf cod under SARA for economic reasons, recovery planning is still a priority for the stock. Population recovery scenarios should consider known external variables, such as the influence of environment and harp seal populations on recruitment and mortality of cod. This could take the form of joint population projections or a stochastic projection that would link recruitment to a random categorical variable related to important predator and environmental variables. Moreover, it may be necessary to link other components of the ecosystem to cod recruitment and mortality if deemed important to the long-term recovery of the stock. Studies of this nature help define the level of uncertainty about recruitment processes for single species, so they can aid development of appropriate process-error models for simulation studies designed to evaluate management strategies.

Acknowledgements

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