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A Framework for the Development of Management Advice
on a Shrimp Stock Using a Bayesian Approach

by

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Abstract

This background document describes the assessment-framework used to generate an assessment of, and management advice for, the West Greenland shrimp stock in 2002 (Hvingel 2002).

Biomass dynamic models based on the logistic function, with and without an explicit term for cod predation were used to describe shrimp population dynamics. Biomass indices from a research survey and standardised commercial catch-per-unit-effort series, catch, cod stock size estimates, cod predation estimates and “priors” of model parameters provided information to the models. The inadequacy of a model to fully describe population behavior and the inevitable errors associated with the observed data series, i.e. observation and process error, were incorporated simultaneously using a state-space modeling framework. A Bayesian approach was used to construct a “posterior” distribution of likelihoods of possible values of model parameters and derived variables relevant for developing management advice.

The model including cod predation proved superior to the basic version, in which the only mortality considered to occur was yield to the fishery.

The document discusses practical and theoretical considerations pertaining to the selection and design of the model and to the Bayesian estimation methods used, and it also explains how the model results may be extended to the construction of management advice.

Introduction

Annual landings of northern shrimp (*Pandalus borealis*) in the North Atlantic have increased from about 100000 tons in the early 1980s to more than 350000 tons in 2001 (Skúladóttir, pers. com.). Although shrimp has become one of the most important target species in these waters, little progress has been made in developing a standardised predictive tool for stock assessment (cf. Stefánsson *et al.*, 1994; Cadrin and Clark, 1999; Savard *et al.*, 1991; Hvingel and Kingsley 2000, Koeller *et al.* 2000, Anon. 2001a+b).

Management advice for most shrimp stocks in the North Atlantic is basically formulated by qualitative assessment of trends in various indices of stock condition in response to the catch history (Anon., 2001a+b; Koeller *et al.* 2000). Typically, biomass estimates and length compositions from research surveys, and commercial catch rate series, constitute the main data source, but additional observations may also be considered, such as predator abundance, temperature etc. Advice is given as an annual Total Allowable Catch (TAC) or as a statement about the sustainability of the current fishing practice as consented by the assessment board. The method of deriving the

advice is not explicitly stated and the uncertainty associated with the process is not quantified. Such methods lack predictive rigour, including formal statements of uncertainty, and are therefore not suited for quantitative comparisons between alternative management options.

A quantitative assessment may be reached through construction of mathematical models describing stock dynamics and their links to collected data and ancillary information. Each model represents one hypothesis about "the state of nature". From the infinite collection of possible models a subset of the most plausible may be chosen based on expert knowledge. An integrated evaluation of inferences about management options from that subset may be considered taking into account the "model uncertainty" of the assessment process. Within each model uncertainty arises from its inability to fully capture the dynamics of the stock and from having to interpret erroneous data. Thus, to capture the full range of assessment uncertainty, three levels of uncertainty need to be considered: 1. model uncertainty, 2. process error and 3. observation error.

Following the ideas of Punt and Hilborn (1997) the first step in the construction of an assessment framework is specifying the alternative hypotheses. This is done through exploring models within three levels of model complexity: 1. the logistic (this paper), 2. the delay-difference (Hvingel and Kingsley, in prep.) and 3. the age-based (Hvingel and Kingsley, in prep.). Within these model types different versions can be investigated by including predation and environmental effects. Process and observation error is incorporated by using a state-space modelling framework (Schnute, 1994) and Bayesian inference (e.g. Gelman *et al.*, 1995) to estimate probability distributions of model parameters.

Age-structured population models that account in great detail for age-dependent growth, growth-dependent recruitment to the fishery, and age-specific fishing and natural mortality are now the standard tool for the assessment of most fish stocks. Such models are critically dependent on accurate annual information on the age and length composition of the stock and the catches. But shrimp have no permanent hard parts to accumulate annual layers and ages cannot be measured. Modal analysis of length distributions (e.g. McDonald and Pitcher, 1979) seems to be inevitably dependent on assumptions about growth rate that are largely unverifiable and leaves large residual uncertainty about converting size distributions into age distributions. This is particularly true for the relatively slow-growing shrimp in northern waters and for the important larger size classes. The use of standard VPA software (e.g. The Lowestoft VPA suite: www.cefas.co.uk) to assess shrimp stocks has not been successful (Savard *et al.*, 1991; Anon., 2001a+b)

The use of non-age-structured models is an alternative. Such models are usually of the stock-production type (Graham, 1935; Schaefer, 1954; Fox, 1970; Pella and Tomlinson, 1969) and describe stock dynamics simply in terms of rates of change of total biomass, rather than by the detail of age-specific growth and mortality of individuals (see Hilborn and Walters, 1992, chap 8. for a review of production models). However, natural mortality is thought to be at least as important as fishing mortality in the dynamics of shrimp stocks, and this limits the application of traditional fishery models. Explicit factors of natural mortality, e.g. predation and physical environment, should therefore be considered when constructing shrimp stock assessment models.

Predation is an important factor in shrimp stock dynamics. Several fish and marine mammal species prey on shrimp (Pedersen and Riget, 1993; Magnússon and Pálsson, 1989; Grunwald, 1998, ref on marine mammals). The Atlantic cod (*Gadus morhua*) co-occurs with northern shrimp, is a bottom-feeding predatory fish, and can attain high biomass densities, qualities which give it the potential for being a controlling predator (Lilly *et al.*, 2000; Berenboim *et al.*, 2000; Stefánsson *et al.*, 1998). The rapid development of the West Greenland shrimp fisheries during the 1970s is thought to be connected to a major decline in the cod stock in that area (Carlsson and Smith, 1978); shrimp fisheries off the Canadian east coast appear similarly to have thrived after the collapse of the 'northern' cod stocks in NAFO Divisions 2J and 3KL. Consumption of shrimp by cod in the Barents Sea is estimated to be about three to four times the amount taken by the fishery (which was about 80000 tons in 2001) (Anon., 2001b). Thus predation by cod may for several shrimp stocks constitute a dominating component of mortality and is therefore an obvious candidate as an explicit natural mortality factor in an assessment model.

The physical environment also affects shrimp populations (e.g. Koeller, 2000; Anderson, 2000) and may be the cause of the rapid changes in abundance seen in some stocks (Anderson, 2000; Apollonio *et al.*, 1986). However, at this stage of modelling, environmental effects were not considered as explicit variables.

The “West Greenland shrimp stock” occurs off West Greenland in NAFO Divisions 0A and 1A–1F. The stock is assessed as a single population (Anon. 2001a) and managed by catch control. A trawl fishery for shrimp started in inshore areas in 1935. After 1970 an offshore fishery developed and landings increased reaching more than 80000 tons in 2001 (Table x). This paper is the first article in a planned series of three on shrimp population dynamic modelling, with the purpose of developing an assessment model for shrimp based on the logistic function, using the West Greenland stock as an example. The models constitute hypotheses about “the state of nature” intended along with the models developed in following papers (Hvingel and Kingsley, in prep.) to enter into an integrated shrimp stock assessment and decision framework able to make use of all available information pertaining to the dynamics of the stock and to provide realistic estimates of uncertainty of the assessment process.

Method

Modelling framework

The models were built in a state-space framework (e.g. Schnute 1994). This time series methodology offers straightforward implementation of process and observation error and great flexibility in the mathematical construction approximating stock dynamics and data-to-stock relations. The State-space modelling technique was introduced in fish stock assessments during the 1990’s (Meyer and Millar, 1999, and references therein).

The state-space conception of a stock dynamic model regards a series of unobserved state values as defining the stock trajectory through time. The states are related to each other and to the data by a set of simultaneous, possibly stochastic, equations. The models were thus defined in terms of sets of parameters (\mathbf{q}), the values of which defined the stock dynamics of the shrimp stock.

A Bayesian approach was used to construct a “posterior” distribution of likelihoods of possible values of model parameters. The posterior gives the probability of a hypothetical set of values for unobserved model parameters (\mathbf{q}), given the data and a “prior” probability distribution for \mathbf{q} , which defines the information available about \mathbf{q} before the experiment was carried out or the observation made. Bayes (1763) restated a general probability identity in the form:

$$p(\mathbf{q} | data) \propto p(data | \mathbf{q})p(\mathbf{q}),$$

where $p(\mathbf{q} | data)$ is the posterior probability distribution, $p(data | \mathbf{q})$ is the likelihood of the data as a function of the values of \mathbf{q} , and $p(\mathbf{q})$ is the estimated or assumed prior probability distribution of the unobservables.

Bayes’s theorem has found limited application in the centuries since it was stated, because integrating the right-hand side of the relationship has been, for most practical applications, an insurmountable problem. However, the rapid increase in readily available computing power, coupled with the development of sophisticated and efficient methods of stochastic integration by sampling, has transformed this situation.

In applying Bayes’s equation to the present problem, the posterior probability distribution of \mathbf{q} is derived by Monte Carlo Markov Chain (MCMC) sampling methods (e.g. Congdon 2001, p. 465-469). The programming framework WinBUGS v.1.3, made available by the Medical Research Council and the Imperial College of Science, Technology and Medicine in England (www.mrc-bsu.cam.ac.uk/bugs; Gilks *et al.* 1994; Spiegelhalter *et al.* 2000), provided a means of specifying and analysing Bayesian models, including selection and implementation of appropriate algorithms. For numerical integration WinBUGS uses “Metropolis-Hastings within Gibbs sampling” (Gilks *et al.* 1996, see also <http://www.mrc-bsu.cam.ac.uk/bugs/>).

State equations

The basic equation was a generalisation of the logistic model of population growth (Richards 1959; Pella and Tomlinson 1969). Its differential form is:

$$\frac{dB}{dt} = Br \left(1 - \left(\frac{B}{K} \right)^{m-1} \right),$$

where B is biomass, K is carrying capacity, and r is the intrinsic rate of growth. m is a shape parameter for the stock-recruitment curve: a value of 2 gives the standard logistic trajectory (often named the ‘‘Schaefer production model’’; Schaefer, 1954). If m takes high values, it implies that density-dependent reductions in population growth do not become significant until high stock levels and *visa versa*.

A discrete form of this model, modified to include fishing mortality and predation by cod, and parameterised in terms of MSY (Maximum Sustainable Yield) rather than r (intrinsic growth rate) (cf. Fletcher, 1978) described the transition from one state, t , to the next, $t+1$:

$$B_{t+1} = B_t - C_t - V_t + IMSY \frac{B_t}{K} \left(1 - \left(\frac{B_t}{K} \right)^{m-1} \right), \quad I = \frac{m}{m-1}$$

B_t is the stock biomass in year t . MSY is the annualised value of the instantaneous maximum sustainable yield rate. C_t is the catch taken by the fishery and V_t is the predation by cod, in year t .

Absolute biomass estimates of most population dynamic models are prone to large uncertainty if no explicit information is available to scale the biomass indices to real stock size. For management purposes therefore it is desirable to work with biomass on a relative scale in order to cancel out the uncertainty of the ‘‘catchability’’ parameter (the scaler). This was accomplished by dividing eq. xx throughout by B_{MSY} , the biomass that produces MSY . This reparametrisation also had the effect of reducing auto-correlation in the chains of values sampled by the Gibbs sampler and thus speed convergence to the posterior distribution (cf. Meyer and Millar, 1999). Finally a term for the process error was applied and the state equation took the form:

$$P_{t+1} = \left(P_t - \left(\frac{C_t + V_t}{B_{MSY}} \right) + \frac{mMSYP_t}{B_{MSY}(m-1)} \left(1 - \frac{P_t^{m-1}}{m} \right) \right) \cdot \exp(\mathbf{n}_t)$$

where P_t is the stock biomass relative to biomass at MSY ($P_t = B_t / B_{MSY}$) in year t . The ‘process errors’, v_t are normally, independently and identically distributed with mean 0 and variance \mathbf{s}^2 .

The basic stock-dynamic model in the absence of fishing and explicit predation has the characteristics that the biomass at MSY is equal to:

$$B_{MSY} = Km^{\frac{-1}{m-1}}$$

and the MSY itself is given by

$$MSY = \frac{Kr}{I}$$

Data and link functions

Two series of biomass indices were available from the monitoring programme on the West Greenland shrimp stock (Table 1). A standardised and combined series of annual commercial vessel catch rates 1976 to 2001, $CPUE_t$, (Hvingel *et al.*, 2000, Hvingel, 2001) and a biomass index obtained by the Greenland trawl survey for the years 1988-2001, $surv_t$, (Kingsley *et al* 2000, Kannevorff and Wieland, 2001). These indices were assumed scaled to real

biomass by the catchability constants, q_c and q_s respectively. Lognormal observation error were applied, \mathbf{w} and \mathbf{k} , and hence these data took the distributions¹:

$$CPUE_t \sim \log N(\ln(q_c B_{MSY} P_t), \mathbf{w}) \text{ for } t \in (1, 2, \dots, n-1) ,$$

$$surv_t \sim \log N(\ln(q_s B_{MSY} P_t), \mathbf{k}) \text{ for } t \in (2, 3, \dots, n)$$

. The error for the final year of the CPUE index was assumed to be 1.5 times the error for the rest of the series, as this data point is an interim one based on fishery data until October (the annual assessment takes place in November). Likewise the first year of the survey was assigned a 50% larger error than the remaining series to account for the learning process:

$$CPUE_n \sim \log N(\ln(q_c B_{MSY} P_n), 1.5\mathbf{w}) , \quad surv_1 \sim \log N(\ln(q_s B_{MSY} P_1), 1.5\mathbf{k})$$

Total reported catch in NAFO Subarea 1 + Div. 0A 1970-2001 (Hvingel, 2001) was used as yield data (Table 1). These data are generally considered very reliable without major discarding problems or misreportings and were therefore entered in the model as error-free.

Estimates of annual consumption of shrimp by cod based on stomach sampling were available for the years 1989-92 (Grunwald, 1998, Table 26). These were reduced by 2,5% to compensate for the difference in size composition taken by the fishery and by cod and linked to the equations of shrimp stock dynamics through a Holling type III functional response function (Holling, 1959) and a series of cod biomass:

$$O_t = cod_t \frac{V_{max} P_t^2}{P_t^2 + P_{0.5}^2} \exp(\mathbf{t})$$

where O_t is total consumption in year t , V_{max} is the maximum consumption of prey per predator (kg/kg) reached at large prey biomass, and $P_{0.5}$ is the prey biomass index at which the consumption is half of the maximum. cod_t is biomass of cod in year t . The error term, \mathbf{t} , is normally, independently and identically distributed with mean 0 and variance \mathbf{e}^2 . Thus the predation is set to depend simultaneously on the shrimp stock biomass, P_t , and on the biomass of the predator, Atlantic cod. This function predicts a sigmoidal response of predation rate to increasing prey density, which essentially states that at intermediate shrimp density the consumption *per predator* increases linearly with prey density, but that at low prey density it approaches zero and at high prey density it has an asymptotic maximum. Shrimp is not regarded as the primary forage for cod if fishes, e.g. capelin (*Mallotus villosus*) (Bereinboim *et al.*, 2000 and Magnússon and Pálsson, 1991) or Arctic cod (*Boreogadus saida*) are available. The relative abundance of shrimp may therefore be expected to have to reach a certain level for cod to switch to this food type.

The cod biomass series 1955-2001, cod_t , was constructed as follows. Absolute estimates of stock size for West and East Greenland stocks combined were available until 1992 when the cod fishery stopped owing to very low stocks (Anon., 1996). For the years 1982-92 these estimates could be partitioned in an East and West component using the relative East/West Greenland survey-based biomass indices. The series were extended back in time by multiplying the total biomass estimates with 0.6 – the calculated average fraction of the total stock occupying West Greenland waters from 1982 through 1992. The years 1993 and forward were constructed by converting the survey indices to absolute biomasses by applying the mean survey/absolute biomass relation for 1990-92.

Priors

Bayesian statistics perceives a set of observations (data) as updating or correcting a prior model of reality. The prior model of reality is summarised in "prior" distributions of model parameter values, which is founded on ancillary knowledge, conceptually pre-existing and independent of the study. The prior distribution for a parameter should

¹ in these equations, the designation $x \sim \log N$ means 'x is distributed as log-Normal'; i.e. the logarithm of x has a Normal distribution

incorporate all external information available. If no prior knowledge is available a low-informative "reference" prior (Kass and Wasserman, 1996) is used.

Prior probability distributions of parameter values may in data-scarce situations (i.e. in most marine population-dynamic modelling) often have important influence on the posterior distribution and therefore on the conclusions drawn from a model. Selection of appropriate priors is therefore an important phase of building a Bayesian model. Distributions of the different parameters in the model interact, and what appears to be a reference prior for one variable may through its interactions with other variables act as an undesirably informative prior for them. Some guidelines for developing priors are given in Punt and Hilborn, 1997, and Gelman *et al.*, 1995.

The choice of distribution for particular priors may in some cases be a matter of taste. The important issue is that the prior has the desired shape for the values covered by the posterior. In practice it is sometimes desirable to truncate the distributions in order not to unnecessarily slow down the sampling process. The limits of the distributions were in those cases chosen to be generously wide so as not to interfere with the posterior.

q_s, q_c (catchability coefficients)

The catchability coefficients, q_c and q_s , scaled the biomass indices of the standardised CPUE and survey series respectively to the absolute biomass estimates. Little prior information about these parameters was available. Thus Reference priors were used. Because the catchability coefficients interacted with the carrying capacity, K , a uniform distribution was not non-informative, and a prior distribution uniform on a log scale from $-\infty$ to ∞ was preferred (Punt and Hilborn, 1997; McAllister and Kirkwood, 1997; Gelman *et al.*, 1995). In practice this was approximated by using $\ln(q_c) \sim U(-15, 1)$ and $\ln(q_s) \sim U(-10, 1)$ (U is the uniform distribution).

MSY (Maximum sustainable yield)

The prior distribution for MSY was given a weakly conservative prior, uniform on a log scale between $\log(35000)$ and $\log(1000000)$. The lower truncation point, at 35000 tons, was considered the most pessimistic estimate of the production capability of this stock by comparison with the catch per unit area supported by the shrimp stock off the Canadian east coast (Parsons pers. comm.). The upper truncation point was arbitrarily chosen high enough not to interfere with the posterior.

m (the shape parameter)

We had no prior information on the shape-parameter, m , for this stock. A uniform prior for m would not be uninformative with respect to the location of B_{MSY} relative to K . To make a reference prior for the ratio B_{MSY}/K , in terms of m , an approximate function was used for the conversion. The curve of m as a function of B_{MSY}/K in the interval $0.37 < B_{MSY}/K < 0.63$ was approximated by $m = a \exp(bP_{MSY}^c)$ with appropriate values of a (0.1817), b (5.1174), and c (1.0938).

B_{MSY}/K was then assigned a uniform distribution on the interval 0.37 to 0.63. Values of B_{MSY}/K below approx. 0.37 ($m < 1$ in eq xx. i.e. beyond the Fox model (Fox, 19xx)) implying that the stock's rate of increase becomes infinite as its size approaches zero, are unrealistic as a characteristic of fish stocks. The upper truncation point was arbitrarily chosen to make the prior symmetric around $B_{MSY}/K = 0.5$.

K (carrying capacity)

The largest catch taken in a year is about 100 thousand tons and this may be taken as a lower bound on K . It was hard to come up with an upper limit to K . However, it seemed, at least in this case where little information on K was available in the data, to be important to prevent sampling of very high, unrealistic, values. Thus an upper limit was constructed as follows: some of the highest densities ever recorded in the survey are around 0.5 kg/m^2 . The total distributional area of the stock is about $120\,000 \text{ km}^2$, much of which has densities well below commercial interest. If as much as 10% of the total area had 0.5 kg/m^2 it yields some 6 000 thousand tons. This was chosen to provide what was thought as a safe upper limit. Instead of using a uniform distribution $U(100, 6000)$ the prior was uniform on a log scale with limits at 4.6 and 8.7 in order to reduce the tendency of the sampler to wander off to high values.

P_1 (starting biomass level)

There is usually little information about the historic size of a stock preceding the time series of biomass indices. In order to overcome this difficulty, it is commonly assumed that $B_1 = K$, i.e. that the stock was, initially, at carrying capacity. However, this assumption may have the effect of imposing an informative prior on K , it is not easy to defend in any circumstances, and it is especially questionable when, as in the present case, the stock had already been fished for some years before the start of the observations and was subject to predation by a fluctuating cod stock. Instead we used the less informative log-Normally distributed prior $P_1 \sim \log N(0.44, 0.2)$ with a mode at about 1.5 in the model without a predation effect, and $P_1 \sim \log N(-0.05, 0.2)$ with a mode at approximately 0.9 when predation was included – the decreased mode acknowledged the presence of a large cod stock prior to the data series.

[P_1 was in this case the biomass level of 1955, i.e. 20 years before CPUE based biomass index series began. With a low-informative prior for the starting biomass The estimates of annual 1956-75 biomass levels are conceptually equal to an iteratively reconstruction constrained on the parameter estimates of the post 1975 series and the catch and cod stock size series (table x).]

$S_w^2 S_k^2 S_n^2 S_t^2$ (error terms)

The priors for the error terms associated with the biomass indices were based on an estimated CV of around 10% for the CPUE-series (Hvingel *et al.* 2000) and about 17% for the survey series (Kingsley *et al.* 2000). The probability distribution of their standard deviations therefore had modes at 0.10 and 0.17 respectively, i.e. their precision were gamma distributed: $1/S_w^2 \sim G(2.5, 0.03)$ and $1/S_k^2 \sim G(4, 0.1125)$ (the gamma distribution, $G(r, m)$, is defined by: $m^r x^{r-1} e^{-mx} / \Gamma(r)$; $x > 0$). The precision for the series of consumption by cod, V , were given a prior $1/S_n^2 \sim G(2.5, 0.03)$ as a result of the expected larger uncertainty associated with the construction of the series. The mode of this distribution corresponds to a CV of around xx%. The precision of the stock size, P , were given a low informative prior $1/S_t^2 \sim G(0.001, 0.001)$.

O_{max} (maximum predation rate)

O_{max} provides an upper limit to the amount of shrimp consumed by cod. The data itself could not be expected to contain much information about this parameter. An informative prior for the largest possible quantity of shrimp (kg) eaten pr. kg of cod was therefore constructed using estimates of growth and food conversion coefficients for cod feed to satiation in laboratory experiments (Björnsson *et al.*, 2001; Björnsson and Steinarsson, in press). A maximum annual weight gain pr. kg fish for each age group was calculated inserting mean weight at age (Anon. 2000, NWWG) and an estimated average water temperature of 2 °C in the growth model (Björnsson and Steinarsson, in press). A food conversion coefficient of 3 (Björnsson *et al.*, 2001) was then applied to convert the weight gain to maximum annual shrimp consumption. Assuming an average population structure of 1975-89 (Anon., 1996) a level for O_{max} was estimated to 3 kg shrimp/kg cod/year. The prior was given a relatively tight distribution of the form $O_{max} \sim N(3, 0.1)$.

P_{50}

The parameter P_{50} is the size of the shrimp stock at which 50% of O_{max} is reached. As O_{max} is supposed to be relatively well determined P_{50} will have an important effect in setting the predation rate $O(P)$. A prior for P_{50} that was approximately non-informative with respect to the predation rate was constructed by a formula equivalent to eq. x.:

$$P_{0.5} \text{prior} = \sqrt{\frac{O_{max} P^2}{o(p)} - P^2}$$

giving $O(P)$ 'sequivalent parameter, $o(p)$, a uniform distribution between 0 and 3, setting $o_{max}=3$ and simulating P to vary between 0 and K by giving p a uniform distribution 0 to 2.

Convergence diagnostics

Conclusions based on an MCMC output depend on the assumption that the chain of sampled values for each parameter can be considered to be an unbiased random sample from the target distribution, i.e. the posterior. A chain is usually serially correlated, and at the start is affected by the initial value assigned to each parameter. Initial values are not necessarily, or even usually, random samples from the posterior distributions. To check that the influence of the initial value had decayed and that the chain had ‘converged’ to a stationary sampling from a constant distribution before data collection began, several diagnostic tools were applied. This was done in S-PLUS 2000 (www.mathsoft.com/splus) using the Bayesian Output Analysis programme (BOA) v. 0.5.0 by Brian Smith (www.public-health.uiowa.edu/boa/), which provides a suite of processing and diagnostic tools for MCMC outputs.

A number of parallel chains with different starting points and with different random number seeds were analysed by the Brooks, Gelman and Rubin convergence diagnostic (Gelman and Rubin, 1992; Brooks and Gelman, 1998) to evaluate if the samples could be considered to have arisen from the target distribution. A stationarity test (Heidelberger and Welch 1983) was applied to individual chains. If evidence of non-stationarity is found this process discards iterations from the beginning of the chain until the remaining chain passes the test. Raftery and Lewis’s (1992) tests for convergence to the stationary distribution and estimation of the run-lengths needed to accurately estimate quantiles was also used.

Model check

In order to check whether the model was a ‘good’ fit to the data, the observations were compared with their predicted distributions. Different goodness-of-fit statistics were computed.

Firstly, we calculated the simple difference between each observed data point and its trial value in each MCMC sampling step. The summary statistics of the distributions of these residuals indicated by their central tendency whether the modelled values were biased with respect to the observations. The dispersion of the residuals was compared with both the classical statistical estimate of the SE of the respective observed value and the modelled collective estimate of the precision of the observation sequence.[what is this??]

Secondly, the overall posterior distribution was investigated for potential effects of model deficiencies by comparing each data point with its posterior predictive distribution (Posterior Predictive Checks; Gelman *et al.* 1995, 1996). Intuitively this is equivalent to running the model backwards to see the data needed to get the suggested result and then judge if that is a realistic scenario.

Simulated sets of observed data, $data_{rep}$, were drawn from the sampling distributions for the observations as output from the model. Therefore, $data_{rep}$ has distribution:

$$P(data_{rep} | data_{obs}) = \int P(data_{rep} | \mathbf{q})P(\mathbf{q} | data_{obs})d\mathbf{q}$$

In this expression the term $P(data_{rep} | \mathbf{q})$ represents the sampling of observations from the distributions set up in the model to define them, and the term $P(\mathbf{q} | data_{obs})$ represents the sampling of the parameters of those distribution from their own *posterior* distributions. If the model fitted the observed data well, the observed data should, collectively, be a ‘likely’ drawing from its simulated distribution, i.e. the observed data and the replicate data should look alike. The degree of similarity between the original and the replicate data points were summarised in a vector of p-values, calculated as the proportion of N simulations in which a sampling of the posterior distribution for an observed value exceeded the value in the input data:

$$p.value = \frac{1}{N} \sum_{j=1}^N I((data_j^{rep}, \mathbf{q}_j) - (data_j^{obs}, \mathbf{q}_j)) \quad ,$$

where $I(x)$ is 1 if x is true, 0 if x is false. Values close to 0 or 1 in the vector *p-value* would indicate that the observed data point was an unlikely drawing from its posterior distribution.

Thirdly, the ‘Conditional Predictive Ordinate’ (Gelfand and Dey, 1994) was calculated as a harmonic mean of the likelihood:

$$CPO_i = \left[\frac{1}{N} \sum_{j=1}^N \frac{1}{p(\text{data}_i | \mathbf{q}_j)} \right]^{-1}$$

where N is the number of MCMC samples. This statistic indicated by small values if the relevant data points were a poor fit to the model.

Fourthly, to compare the fit of the two models we calculated the deviance (Gilks et al. 1992) as the sample mean of the log-likelihoods times -2 .

$$\overline{DEV} = \frac{1}{N} \sum_{j=1}^N (-2) \sum_i \ln(p(\text{data}_i | \mathbf{q}_j))$$

and the negative cross-validators log-likelihood (Gelfand and Dey, 1994):

$$NCL = \sum_i \ln \left(\left[\frac{1}{N} \sum_{j=1}^N \frac{1}{p(\text{data}_i | \mathbf{q}_j)} \right]^{-1} \right)$$

again N is the number of MCMC samples. These statistics both give small values the better the fit of the model.

Results and considerations with reference to the modeller

Two models were investigated. In each run BUGS was set up to do 550000 iterations, however only recording every 50th to compensate for serial correlation within the chains of some of the sampled parameter values. The first 1000 samples of the recorded chain were discarded for “burn-in” leaving 10000 samples as the final result. Convergence diagnostics were calculated for the parameters listed in Table 3 to confirm that the model and sampling set-up was appropriate to ensure convergence.

Model 1 (without explicit predation effect)

A Bayesian model, similar to that described above, but omitting all observations, parameters, equations and distributions concerning predation on shrimp by Atlantic cod, was fitted to the data series on CPUE, survey and catch. This model was similar in concept to that fitted by likelihood methods in Hvingel and Kingsley (2000). The run-time for this model was approx. 4 hr’s on a 700 MHz-laptop. The use of a variable shape parameter, m , for the stock recruitment curve rather than fixing it at 2 (= the Schaefer model), more than doubled the run-time.

Judged from the generated posterior distribution the data did not contain sufficient information about K to improve much on the prior assumption about this parameter (Fig 2). A mode was however evident at around 1 mill. tons but the used prior truncated at 6 mill. tons was seen to interfere with the posterior. It is not an uncommon phenomenon that logistic population-dynamic models fitted to real fisheries data are unable to differentiate between a large unproductive stock and a small productive one but still may produce a reasonably good determination of MSY , especially if the fishery has been stable with catches near MSY . Also we had no strong evidence of what the upper limit of the carrying capacity might be. So instead of discarding this model right away, we changed the upper truncation point of the K prior to an arbitrarily chosen value of 15 million tons. This would still interfere with the posterior for K , but increasing the upper limit further did not seem to influence the posteriors of the other parameters in the model significantly.

In this setup the model was able to produce a reasonable simulation of the observed data (Figure 4). The probabilities of getting a more extreme observation than the realised ones given in the two data series on stock size

were in the range of 0.11 to 0.5 (Table 3) i.e. the observations did not lie in the tails of their posterior distributions. For the CPUE series the data point of 1987 were suggested by a low CPO to be a relatively poor fit to the model. Minor problems capturing the extremes of 1979, 1982 and 2001 were also indicated by these points having relatively large residuals and small CPO's (Table 3). The survey series was generally less well estimated, the 1991 and 1994 values showing the largest residual's and smallest CPO's.

Some of the parameters showed high linear correlation (Table 4). The catchabilities (q_c and q_s) were negatively correlated with the parameter for carrying capacity, K , and to some extent with MSY . MSY and K were only slightly positively correlated.

For the parameters m (represented by B_{msy}/K), K and P_I the posterior distributions tended to approximate the input priors (Fig. 2). The posterior for MSY was positively skewed and showed a mode at 90 000 tons and upper and lower quartiles at 82 700 and 187 000 tons giving a more optimistic view of MSY than assumed in the prior. The catchabilities, q_s and q_c , showed marked peaks at 0.045 and 0.00019 respectively but had relatively wide posterior distributions. The estimated CV of the observed CPUE series had a median at about 8.4% and for the survey series at 14.9%. The process error, σ , had a median of 10.3% (Table 4).

Model 2 (cod predation effect included)

Entering a predation effect in the model only had minor influence on the model diagnostics (Table 3 and 5) - a slightly better fit for the CPUE series was however indicated. The probabilities of getting a more extreme observation than the realised ones were in the range of 0.12 to 0.5 (Table 5). For the CPUE series it was still the peaks in 1979, 1982 and 1987 that had the largest log-residuals and smallest COP's. Similarly, the greater variability of the survey series was still less well captured with the values of 1991 and 1994 being the most obvious deviations. Large correlations among parameters still prevailed (Table 6).

However, precision of the key parameters had improved substantially. The mode of the MSY posterior was at 94000 tons not far from that of model 1 (Fig. 3) but the lower quartile was at 88000 tons and the upper at 111000 tons (Table 7) - a decline in inter quartile range of that parameter from 86% to 24%. The posterior of the K parameter now had a more peaked distribution with a mode around 740 000 tons (Fig. 3). The catchabilities, q_s and q_c , were larger and also more precisely estimated than in model 1 showing modes at 0.52 and 0.0022 respectively. The posterior distribution for B_{msy}/K , approximately uniform in the absence of predation, changed to favour values at the lower end of its range i.e. values approaching the Fox form of the logistic model (Fox, 1970). The posterior of the initial state, P_I , still resembled the input prior.

The estimated CV's of the observed biomass indices, k and w , were similar to those estimated in model 1. However, the posterior for the process error, n , had, in line with the observations noted above, decreased significantly from mode 0.094 to 0.071. The posterior for the CV of the observed cod biomass series, t , markedly updated the prior expectations (Fig. 3) having a mode at 0.28.

The parameter set to be the main determinant of cod predation rate, P_{50} , was markedly updated with a posterior showing a mode at 3.63. As expected there was no information in the data about O_{max} and the posterior copied the prior. The estimated median annual consumption by cod 1956-2001 ranged from 200-100 000 tons - the relative interquartile range was for most years around 50% (see Fig. 4).

Model selection [this should prob. Go to disc.section]

The goodness of fit statistics (table 3+6) did not provide clear advise on model selection. However, large differences in the precision of estimates of central parameters were evident (Fig. 2+3). The process error was reduced by 1/3 by the inclusion of the predation effect and the relative IQ-range of MSY and K went down by about 2/3 (Table 4+8). This greatly reduces uncertainties in projections of future developments of stock biomass (figure x) - at least during the current regime of extreme low cod stock levels where the observation error associated with the cod biomass series only give a minor contribution to the variability of the projected shrimp stock sizes.

The two models also produced different simulations of likely stock biomass trajectories back in time before 1976 (Figure x). Having only the time-series of catch available as input data for that period, model 1 predicts a more or less constant stock size around the high level of the 1976 value (Figure x). Model 2 using both catch and cod data, predicts the shrimp biomass to have been at about half the size during the period of high cod abundance in the 1960's as compared to the current 1976-2001 level. This scenario agrees with the general belief that the stock in those years was at a lower level (S. E. Horsted, pers. comm.).

The aim of this modelling exercise may be summarised as to define the quadratic function that describes the productive potential of the stock at various stock sizes (fig, 5). How well this curve is defined by the data may be visualised by plotting the stock size and corresponding production as calculated directly from the observed biomass indices. This was done by applying the MCMC sampled catchabilities to the actual index values to obtain biomass estimates. Production was calculated by subtracting biomass in the current year from biomass in the next and then adding catch and if necessary estimated predation. Although only a minor difference is seen in the estimated median stock-recruitment curve the larger variability of the model 1 estimates is obvious (fig.xx). Further model 2 yields more points in the high leverage area around the MSY-biomass level.

Results and considerations with reference to assessment and decision making

State of the stock

During the period of the developing offshore fishery (since the early 1970's) the estimated time series of median biomass level, P_t , ranged from about 1.1 to 1.7 and the probability that each successive annual shrimp biomass ratio had been greater than the biomass at MSY was calculated to be larger than 0.92, i.e. under this hypothesis (model 2) it seemed likely that the stock had been maintained above its MSY level throughout the history of the modern fishery.

As mentioned in the methods section biomass is presented as scaled to B_{msy} to cancel out the variability in q . For the same reasons estimates of mortality caused by cod predation and fishery is scaled to Z_{msy} (the combined fishing and predation mortality that yields MSY). In this case the variability (ratio of the interquartile range to the median) of the B-ratio was on average 67% lower than the absolute estimate of B . The Z' -ratio had about 19% lower relative interquartile range as compared to the absolute estimates of Z .

Probability distributions of quantities like mortality or other statistics relevant for the assessment/ management procedure but not readily available as model parameters, may also be generated by the MCMC sampling process if they can be derived from the existing parameters of the model. This is done by adding the appropriate equations to the model code. The equations added for generating posteriors of the Z' -ratio were:

$$Zratio_i = \frac{Z_i}{Z_{MSY}} = \frac{-\ln\left(\frac{B_i - (C_i + V_i)}{B_i}\right)}{\frac{MSY}{B_{MSY}}}$$

In the derived biomass vs. mortality perspective (Fig 6) the shrimp stock may be seen as having existed during two different regimes: one with high and one with low cod abundance. The trail of the medians of these two parameters starts in 1956 and cycles around at a relative high mortality and low biomass level during the years of high cod abundance. The cod stock then declines, mortality starts to decrease and shrimp stock biomass increases and begins cycling in the left-upper corner of the graph.

Risk of exceeding a reference point

Often reference points of stock or fishery status are defined as guidelines of management - e.g. to comply with the concept of "precautionary approach" (FAO, 1996). The probabilities of transgressing the chosen limits in response to different management options may also readily be derived within this modelling framework. E.g. what is the risk of exceeding the reference points in five years under a given regime of catch and cod predation? This is done by

increasing the number of states by the required projection period—in this case to N+5—and then adding the values pertaining to the management option under investigation—typically a certain series of annual catch figures. The risk is then simply the relative frequency of the MCMC sampled values that exceed the reference points and can be calculated by

$$risk_i = \frac{1}{N} \sum_{j=1}^N I(limit - B_{ij}) ,$$

where *limit* is the value of the reference point, B_{ij} is the j^{th} sampled value of the state B_i . $I(x)$ is 1 if x is true, 0 if x is false. This function is available in WinBUGS as the “step function” (Spiegelhalter *et al.* 2000).

NAFO (North Atlantic Fisheries Organisation) define the limit reference points for mortality, F_{lim} , as equal to F_{MSY} . If that is exceeded the stock is “overfished”. B_{lim} is the spawning stock biomass below which unknown or “low” recruitment is expected (Anon., 1998). Not to cross Buffer reference points, B_{buf} and F_{buf} , are also defined to provide a buffer zone to ensure that there is little probability that the limits reference points are crossed. The distance of the buffer reference point from the limit reference should reflect uncertainty i.e. distance should be greater the greater the uncertainty in the determination of the limits. In this stochastic state-space Bayesian approach to derive fisheries advice there is little need for the buffer reference points as the risk of exceeding the limit reference is directly calculated and uncertainty associated with the entire process is taken into account.

The limit ref points for the Z-ratio is 1 according to the NAFO convention, i.e. $Z_{lim}=1$. Defining a limit reference point for the biomass ratio for actual use in the assessment needs thorough considerations, which is beyond the scope of this paper. For demonstration it was chosen as having a normal distribution with a mean of 0.4 and a standard deviation of 0.1: $B_{lim} \sim N(0.4, 0.1)$ in the interval $0.4, \text{inf.}$ - and then the appropriateness of the terminology: reference “point”, of course starts to fade. However using a probability distribution instead of a point estimate accommodates the uncertainty associated with the determination of where the border to the dangerous area actually lies.

An optional catch series of 85, 90, 100, 110 and 120 thousand tons for the next five years were investigated and the following decision table could be created:

Optional Catch ('000 tons)	85	90	100	110	120
Risk(non long term sustainability)	0.03	0.17	0.56	0.79	0.89
Risk(Biomass in 2006 < BMSY)	0.00	0.03	0.07	0.17	0.32
Risk(Biomass in 2006 < Limit biomass)	0.00	0.00	0.00	0.00	0.01
Risk(Mortality in 2006 > Limit mortality)	0.03	0.11	0.33	0.59	0.73

The scenario of future shrimp stock development during a period of zero cod may easily be made more realistic in terms of uncertainty by entering probability distributions for the expected annual size of the cod stock. These probability distributions can be based on the assessments results for that stock or e.g. constructed for investigating “worst case” scenarios. Thus when evaluating future events, premises of various kinds may be entered in the model and risk associated with management actions can be quantified.

Discussion

No matter the methods used, the fitting of stock-recruitment models based on sigmoidal stock-trajectory curves to fisheries data is still constrained by the amount of information about system behaviour that can be extracted from the given perturbation history. In the Bayesian framework fundamental absence of information in the data will just yield

posteriors as a copy of the input priors and thus not provide any update of the initial hypotheses. For the data to carry information on all the parameters of the model it requires that the biomass should vary widely both above and below B_{MSY} . If the available data series does not span these conditions, problems in fitting stock-production models by *any* method can be expected (see Hilborn and Walters, 1992, p. 311-319 for further discussion of potential fitting problems).

The available time series of indexed stock sizes for the West Greenland shrimp stock does not cover the entire range of the stock/production function (Fig 5). It looks as though the stock size has been fluctuating above B_{MSY} for the period 1976-2001. However, in the applied parametrisation both the starting point and the location of the maximum production of the stock-recruitment function is fixed and thus the suggested regression line in the figure is not as speculative as it might look at first sight.

Even though the conditions for estimation of some parameters are not optimal it may still be possible to get good estimates of parameters relevant for the management of the stock. Fortunately MSY is the easiest single parameter to estimate. If the range of biomass includes B_{MSY} , good estimates of the MSY can be obtained independently of other parameters. In some cases, this can be done even if the range of biomass merely approaches B_{MSY} from one side or the other as seen in this case. Model 2 yields estimates of production of stock sizes close to B_{MSY} and of a larger part of the upper range of possible stock sizes. We conclude that the lack of contrast in the stock dynamics in this case is not an impediment for obtaining reasonable estimates of management relevant parameters. However, an adaptive management program designed to further explore the production potential of the stock, i.e. investigating stock response to higher quotas, would enable us to provide firmer statements about the production potential of the stock. The security of adaptive management is, however, dependent on having confidence in the basic model of stock dynamics.

The goodness-of-fit statistics (table 3+6) indicated no difference in the ability of the two models to reproduce the observed biomass indices. But even though only minor differences were seen in the shape of the estimated median stock-recruitment curve the larger variability of the model 1 estimates was apparent (fig.5). The process error was reduced by 1/3 by the inclusion of the predation effect and the relative IQ-range of MSY and K went down by about 2/3 (Table 4+8). This greatly reduces uncertainties in projections of future developments of stock biomass (fig. 4) - at least during the current regime of extreme low cod stock levels where the error contribution from the estimation of predation is small.

The two models also produced different simulations of likely stock biomass trajectories back in time before 1976 when the CPUE-series starts (Figure 4). Having only the time-series of catch available as input data for that period, model 1 predicts a more or less constant stock size around that of the 1970-80's. The late 1960's mark the end of a 50-year period of high cod abundance at West Greenland (ref: ICES cod and climate). Model 2 estimates of the shrimp stock size during that period to be about one third of the current size – and in the mechanics of the model this is a result of cod predation. There are anecdotal information confirming that the shrimp stock was lower at the time (S. E. Horsted, pers. comm.) but no firm holding points to set the actual level.

The posteriors of MSY from the two models covered the same range of values however, the difference in precision by including predation was significant (fig. 2+3). The informative prior used for MSY had little influence on the posterior. Only minor changes to its the right tail could be noticed by imposing an alternative non-informative uniform prior from 0 to 500 000 tons and posteriors of other parameters remained practically unchanged.

The parameter K could not be determined with much precision using model 1. The posterior distribution was approximately uniform between its prior defined upper and lower limits and proved quite sensitive to the formulated prior. As indicated in figure x negative production, indicating that K has been exceeded and a density dependent stock reduction is taking place, occur at a wide span of stock sizes. An informative prior for q or K would greatly improve conditions, however, such prior knowledge were not available. Even trying to specify an upper limit to K was a somewhat speculative business. In model 2, K is much tighter defined (figure 3). The estimates of catchability are less variable and part of the apparently low or negative production estimated in some years by model 1 (fig. 5) may now be accounted for by predation rather than by an intrinsic density dependent regulation alone.

The shape parameter, m , was not well determined by either of the models - as could be expected (fig. 2+3). This parameter is closely related to the ratio of MSY to K , and presents similar estimation problems. To get

information on m would require the fishery record to span stock levels from close to carrying capacity to below $MSYL$, and this apparently has not occurred. For model 1, the indeterminance of K precludes estimating m . In model 2, where a distinct distribution of K could be estimated, low values of m gained a relative larger likelihood i.e. the stock recruitment curve was slightly squewed to the right suggesting that the density-dependent reduction of production becomes effective at lower stock size (fig.3).

For both models the marginal posterior distributions of the initial biomass P_1 , tended to approximate the input priors whether these were 'uninformative' or not (Fig. xx). In our models the initial biomass state was, contrary to typical practice when fitting production models, placed several years before data on relative abundance was available. Thus a potential strong signal from the data about stock sizes historic to the CPUE-series would be given off as information about trends in the entire series of stock development rather than just defining the first state of the series.

So the question is not as much whether the data is able to provide an update of the prior for P_1 , but whether the model and the trajectory of biomass states is sensitive to changes in this prior: They were not. E.g. giving P_1 a prior uniform between zero and 2 only made small changes in the estimates of other parameters.

The shapes of priors are more or less subjectively determined by the modeller and are therefore candidates for discussion in the same way as are the reliability of traditional data entries. Overall the model 2 showed low sensibility to changes in prior distributions and in particular for the parameters to be used in the assessment i.e. MSY , B -ratio, F -ratio,, , .

The model estimated the median annual consumption by cod 1956-2000 in the range of 200 tons to about 100000 tons, which is in the same order of magnitude as the catches taken by the fishery (Fig 4). Predation by cod on shrimp in the waters off West Greenland (Sidorenco, 1962; Grunwald, 1998) and elsewhere in the North Atlantic (Lilly et al., 2000 and references therein) has been documented, but little information were available for external validation of the model-estimated quantities consumed. Thus even though there are great incitements for a considerable predation effect from cod the mechanics behind the shrimp-cod correlation is not fully known and could for that reason also partly be attributed to stock responses to the same environmental conditions (Lilly et al 2000).

In the light of the stomach investigation by Grunwald (1998) the estimates of O_{max} of 3 kg /kg looks reasonable. Grunwald (1998) calculates a daily ration of 0.4-0.9% bodyweight per day 1989-1992. Shrimp made up 12-37% of the diet, which implies that an average kilo of cod ate 0.2-1.2 kg of shrimp per year. The stock size corresponding to these levels of predation rate yielded estimates of P_{50} with a median of 3.8 saying that concentrations well above estimated carrying capacity is needed for even reaching half the maximum predation rate. In practice this means that we are only dealing with the left half of the sigmoidal functional response curve.

The need for including explicit factors of mortality in shrimp assessment models other than fishing mortality as responsible of variation in shrimp survival has been stated several times in various workshop or assessment reports (e.g. ices work group 1992, pandalid shrimp symp 2000 ACFM 2002). However this advice has so far only been implemented in the assessment of shrimp in Icelandic waters. This partly stems from the fact that predation may have a complex mode of operation (e.g. Bax, 1998) and the lack of suitable data.

The attractive fit of the version of the model that includes cod predation appears to be due largely to the coincidence of a short-lived resurgence of a cod stock with a steep decline in shrimp CPUE in the very late 1980s. This is a 'one-point correlation'. While it is universal experience that cod are in very fact serious predators on shrimp and unquestionably affect, even control, shrimp stocks, it would be helpful if the coincidence of high cod stocks with decline in shrimp density in West Greenland could be confirmed by more than one data point. Otherwise, it remains a question whether this was cause and effect, or simple coincidence.

If the cod predation fit is driven by this coincidence, based on a single occurrence, it follows that the precision with which the parameters of the predatory response are estimated may be misleading, derived from a fit to a single point.

For comparison a similar model (Hvingel and Kingsley 2000) was run in the ASPIC (Prager, 1994) estimation framework. ASPIC minimises least squares to find best-fitting point estimates given the data, and error is attributed to observations only. 25% percentiles are calculated by a bootstrap procedure (Prager, 1994). The MSY point

estimate from ASPIC is 130000 tons whereas the comparable mode of the Bayesian *MSY* posterior is about 95000 tons. The catchability estimates from ASPIC are also higher. The hypothesis about the “state of nature” arising from this estimation framework is one of a small productive stock while the Bayesian model 1 sees the stock as larger and less productive. In the ASPIC framework the production model was only able to capture the overall trend in the biomass indices (Fig. 4).

It is however difficult to compare parameter estimates from ASPIC with those obtained in the present model, which uses more sophisticated likelihood functions and fitting methods.

“Traditional” assessment models framework is often found to lack flexibility in terms of which data can be allowed to enter the assessment and in terms of the equations of population dynamics and data links, which dictate a fixed general behavioural pattern through time even though it is known that for some individual years it does not comply. An alternative approach is to scrap the population dynamic equations and data link functions and use a multi-indicator system as guidance for a harvest strategy. This was recently introduced as the “Traffic light” approach in the management of some Canadian shrimp stocks (Koeller *et al.* 2000). Even though it is not fully explicitly stated, such “synthesis” (Hilborn and Walters, 1992) - type of assessments however still need a model to interpret and integrate the comprehensive list of indicators. Going beyond simple averaging of the indicators, which has its pitfalls (Hilborn and Walters, 1992; Schnute and Hilborn, 1993), the contours of a very complex model seems to emerge. Index-based assessment methods that lack an underlying model have problems in identifying duplications and correlations in the set of indicators being synthesised.

Another relevant criticism of the traditional assessment methods is the use of single-species perspectives, and in many cases neglecting interaction with the surrounding physical and biological environment. However, even if this is the right approach in the eyes of god, moving to full-scale ecosystem models for estimating the production potential of a particular element of that system will yield models at least as complex as the implicit “Traffic light” model and have immense demands for data and knowledge. A simple model in a state-space Bayesian framework may have much to offer in respect of satisfying both the Traffic-light and ecosystem people. In this approach we may stay with a relative simple “main effects model” but still have a framework that can accommodate many types of data and also take ecosystem effects into account.

The state-space model allows for flexibility of the population dynamic hypotheses. In fact as each state (stock condition of a year) is treated as an individual parameter, the transitions from one year to the next might—in an extreme case - all follow different hypotheses of population dynamics, and vice versa for the data link functions. In practice this flexibility is more likely to translate into minor corrections of the general set of equations e.g. to account for an observed atypical recruitment variation, temporary change in discarding practise, a year of extreme temperatures etc. All of the collected data that might not find a direct way into the assessment model as traditional “input data” might still contribute to our description of stock development as such modifications.

A significant strength of using Bayesian methods in the data-poor area of fish stock assessments, is their ability to incorporate knowledge outside the data series of catch, abundance etc.. The Bayesian approach offers a conceptually elegant way to incorporate ancillary knowledge in a model as prior distributions of model parameters. If informative priors can be constructed, based on extraneous information for one or more of the parameters that are poorly defined by the main data series acting through the fitted model, it may significantly boost the ability to estimate. All forms of data ranging from the hard quantitative type, as those obtained through extensive surveys or logbook analyses, to pure anecdotal information can be accepted. A lot of such information with relevance to stock dynamics, data precision or link functions are often available for the assessment. This typically includes, information on stock demographics from length frequency or sex distributions, oceanographic or other environmental data, geographical distribution, fishing pattern etc. All though this is not explored to its full content in this paper all such information may in principle easily be integrated (Hvingel and Kingsley, in prep.).

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Table 1. Input data series: catch by the fishery and a standardised index of their catch-per-unit-effort (CPUE), shrimp biomass index from research survey, cod biomass and estimated consumption of shrimp by cod.

Year	Catch (‘000 tons)	CPUE (index)	Survey (index)	Cod (‘000 tons)	Consump. (‘000 tons)
1955	5			1729.3	
1956	5			1662.5	
1957	5			1286.1	
1958	5			1333.1	
1959	5			1294.3	
1960	5			1589.2	
1961	5			1591.9	
1962	5			1459.7	
1963	5			1448.6	
1964	5			1457.0	
1965	5			1348.4	
1966	5			1386.9	
1967	5			1241.8	
1968	5			877.5	
1969	5			535.9	
1970	8.6			392.7	
1971	9.4			334.9	
1972	9.7			227.5	
1973	12.6			136.8	
1974	22.0			85.8	
1975	37.9			62.9	
1976	50.1	1.232		133.0	
1977	42.1	1.155		122.4	
1978	34.5	0.913		120.3	
1979	35.2	0.826		135.3	
1980	46.0	0.994		106.9	
1981	44.8	0.948		103.6	
1982	44.6	1.212		135.1	
1983	46.8	1.043		87.5	
1984	43.4	0.983		52.7	
1985	54.5	1.036		30.6	
1986	63.1	1.090		41.4	
1987	63.7	1.364		231.0	
1988	60.3	1.016	216.8	307.0	
1989	65.7	0.816	199.6	191.6	84.8
1990	69.4	0.779	213.9	57.5	8.5
1991	75.9	0.762	146.3	7.4	1.0
1992	86.8	0.835	202	8.4	2.3
1993	75.6	0.833	232.7	0.8	
1994	76.6	0.781	249.5	0.3	
1995	70.7	0.851	201.1	0.1	
1996	69.2	0.886	211.9	0.8	
1997	64.5	0.856	185.3	0.6	
1998	66.1	0.970	263.1	0.3	
1999	76.5	1.031	251.5	0.5	
2000	76.5	1.154	236.1	1.3	
2001	83.5	1.200	309.2	5.8	

Table 2. Stochastic surplus production model of the dynamics of the West Greenland shrimp stock incorporating predation by Atlantic cod to be solved using Bayesian inference. “~” means “distributed as”, $N(\mathbf{m}, \mathbf{S}^2)$ is the normal distribution with mean \mathbf{m} and variance \mathbf{S}^2 . Correspondingly, LN is the lognormal distribution, G is the gamma distribution and U is the uniform distribution.

Observables, data ($t = (1, \dots, T)$)

- (a) $CPUE_t = q_c B_{MSY} P_t \exp(\mathbf{w}^2)$
- (b) $surv_t = q_s B_{MSY} P_t \exp(\mathbf{k}^2)$
- (c) $V_t = cod_t \frac{O_{\max} P_t^2}{P_t^2 + P_{0.5}^2} \exp(\mathbf{t}^2)$
- (d) $cod_t = cod_t$
- (e) $C_t = C_t$

Unobservables, q

States $t = (1, \dots, T)$:

- (f) $P_t \sim LN(\log(0.95), 0.04)$, $t = 1$
- (g) $P_t = \left(P_{t-1} - \left(\frac{C_{t-1} + V_{t-1}}{B_{MSY}} \right) + \frac{mMSYP_t}{B_{MSY}(m-1)} \left(1 - \frac{P_{t-1}^{m-1}}{m} \right) \right) \exp(\mathbf{n}^2)$, $t = (2, \dots, N)$

Priors for:

-Parameters defining stochastic behavior

- (h) $1/\mathbf{s}_w^2 \sim G(2.5, 0.03)$
- (i) $1/\mathbf{s}_k^2 \sim G(4, 0.1125)$
- (j) $1/\mathbf{s}_t^2 \sim G(0.001, 0.001)$
- (k) $1/\mathbf{s}_n^2 \sim G(5, 0.22)$

-Parameters relating biomass indices to real biomass

- (l) $\log q_s \sim U(\log(4.54e-05), \log(1.5))$
- (m) $\log q_c \sim U(\log(3.06e-07), \log(1))$

-Parameters defining predation rate

- (n) $O_{\max} \sim N(3, 0.01)$
- (o) $P_{0.5} \sim LN(\log(0.59), 2.27)$

-Parameters of stock production

- (p) $m = 0.18172 \exp(5.11737 P_K^{1.09382})$ corresponding to: $P_K \sim U(0.37, 0.63)$
- (q) $MSY \sim LN(\log(90), 1)$
- (r) $\log K \sim U(\log(100), \log(6000))$

Joint prior density, $p(\mathbf{q})$

$$(s) p(\mathbf{q}) = p(K, MSY, m, q, q_s, V_{\max}, P_{50}, P_{0.5}, \mathbf{s}_w^2, \mathbf{s}_k^2, \mathbf{s}_t^2, \mathbf{s}_n^2) p(P_I) \prod_{t=2}^N p(P_t | P_{t-1}, K, MSY, m, \mathbf{s}_t^2)$$

Sampling distribution, $p(\mathbf{data}|\mathbf{q})$

$$(t) p(\mathbf{data}|\mathbf{q}) = \prod_{t=1}^N p(CPUE_t, surv_t, cod_t, V_t | P_t, q, q_s, \mathbf{s}_w^2, \mathbf{s}_k^2, \mathbf{s}_n^2)$$

Joint posterior probability density, $p(\mathbf{q}|\mathbf{data})$

$$(u) p(\mathbf{q}|\mathbf{data}) \propto p(\mathbf{q})p(\mathbf{data}|\mathbf{q}) \quad (\text{Bayes Theorem})$$

Table 3. Residuals (% of observed value), probability of getting a more extreme observation, conditional predictive ordinate (CPO), deviance and the negative cross-validatory log-likelihood (NCL) for estimates of model 1 (see methods section for further explanation).

Year	CPUE-series			Survey-series		
	resid.(%)	p.extreme	CPO	resid.(%)	p.extreme	CPO
1976	-4.7	0.34	1.5			
1977	-4.5	0.33	2.0			
1978	4.8	0.34	2.5			
1979	8.9	0.21	1.3			
1980	-1.9	0.43	2.8			
1981	5.0	0.32	2.2			
1982	-8.5	0.20	0.8			
1983	0.7	0.47	3.0			
1984	3.7	0.36	2.7			
1985	1.2	0.46	3.0			
1986	0.5	0.47	2.8			
1987	-13.2	0.11	0.1			
1988	-1.7	0.43	3.0	11.9	0.25	0.7
1989	5.0	0.33	3.1	4.2	0.40	1.1
1990	4.0	0.36	3.7	-8.0	0.31	0.9
1991	0.7	0.47	4.2	27.4	0.07	0.3
1992	-1.3	0.45	4.0	-0.9	0.48	1.2
1993	1.9	0.43	3.8	-11.4	0.23	0.7
1994	7.9	0.23	2.0	-17.9	0.12	0.3
1995	0.2	0.50	4.0	3.0	0.42	1.1
1996	-1.2	0.45	3.8	0.4	0.48	1.1
1997	2.3	0.42	3.7	14.8	0.20	0.8
1998	0.5	0.47	3.5	-10.0	0.26	0.7
1999	0.1	0.50	3.3	-0.4	0.50	0.9
2000	-5.0	0.31	2.0	12.4	0.24	0.7
2001	-4.2	0.36	1.0	-9.7	0.27	0.5
Dev. mean	-44.2			185.5		
NCL	-21.5			68.9		

Table 4. Significant correlations ($p < 0.01$) among parameters of model 1.

	<i>K</i>	<i>MSY</i>	<i>P[1]</i>	<i>P[48]</i>	<i>Pmsy</i>	<i>q</i>	<i>qs</i>	<i>w</i>	<i>n</i>
<i>MSY</i>	0.09								
<i>P[1]</i>	n.s.	n.s.							
<i>P[48]</i>	-0.21	0.39	0.08						
<i>Pmsy</i>	n.s.	-0.09	n.s.	0.06					
<i>q</i>	-0.61	-0.26	n.s.	-0.09	-0.05				
<i>qs</i>	-0.61	-0.26	n.s.	-0.09	-0.05	1.00			
<i>w</i>	0.04	n.s.	n.s.	n.s.	n.s.	n.s.	-0.04		
<i>n</i>	n.s.	n.s.	n.s.	n.s.	n.s.	0.08	0.09	-0.26	
<i>k</i>	n.s.	n.s.	n.s.	-0.05	n.s.	n.s.	n.s.	n.s.	-0.06

Table 5. Mean, standard deviation and 25, 50, and 75 percentiles of MCMC samples from the posterior distribution for selected parameters in model 1.

Parameter	Mean	sd	25%	Median	75%
<i>K</i>	4456	3596	1723	3212	6121
<i>MSY</i>	146.8	93.3	82.7	121.2	187.0
<i>P[1]</i>	0.803	0.162	0.688	0.787	0.900
<i>P[48]</i>	1.796	0.537	1.477	1.785	2.116
<i>Bmsy/K</i>	0.501	0.075	0.436	0.501	0.566
<i>q</i>	5.6E-04	5.2E-04	2.3E-04	4.0E-04	7.0E-04
<i>qs</i>	0.137	0.127	0.056	0.098	0.171
<i>w</i>	0.086	0.017	0.074	0.084	0.097
<i>n</i>	0.104	0.025	0.087	0.103	0.120
<i>k</i>	0.152	0.026	0.133	0.149	0.167

Table 6. Residuals (% of observed value), probability of getting a more extreme observation, conditional predictive ordinate (CPO), deviance and the negative cross-validators log-likelihood (NCL) for estimates of model 2 (see methods section for further explanation).

Year	CPUE-series			Survey-series		
	resid.(%)	p.extreme	CPO	resid.(%)	p.extreme	CPO
1976	-7.1	0.25	1.0			
1977	-7.6	0.23	1.5			
1978	6.1	0.28	2.6			
1979	13.1	0.12	0.6			
1980	-0.7	0.47	3.3			
1981	5.9	0.28	2.4			
1982	-10.2	0.15	0.8			
1983	-0.6	0.48	3.4			
1984	3.9	0.34	3.1			
1985	3.4	0.37	3.0			
1986	3.8	0.35	2.7			
1987	-11.0	0.14	0.4			
1988	-2.3	0.41	3.3	11.8	0.25	0.7
1989	2.9	0.37	3.8	2.9	0.43	1.2
1990	-1.1	0.46	4.7	-11.9	0.21	0.7
1991	-0.6	0.46	4.6	26.3	0.08	0.4
1992	-1.5	0.44	4.5	-0.6	0.48	1.2
1993	-0.2	0.50	4.4	-12.7	0.21	0.6
1994	7.6	0.23	2.3	-17.7	0.12	0.4
1995	0.2	0.49	4.4	3.6	0.41	1.1
1996	-0.7	0.46	4.1	1.5	0.46	1.1
1997	4.5	0.34	3.6	17.8	0.16	0.6
1998	1.2	0.46	3.8	-8.9	0.29	0.7
1999	1.2	0.45	3.6	1.4	0.47	0.9
2000	-4.9	0.31	2.4	13.2	0.22	0.7
2001	-5.3	0.32	1.3	-10.2	0.27	0.5
Dev. mean	-55.2			186.4		
NCL	-23.5			69.0		

Table 7. Significant correlations ($p < 0.01$) among parameters in model 2.

	<i>K</i>	<i>MSY</i>	<i>Omax</i>	<i>P1</i>	<i>P48</i>	<i>P50</i>	<i>Pmsy</i>	<i>q</i>	<i>qs</i>	<i>w</i>	<i>n</i>	<i>k</i>
<i>MSY</i>	0.65											
<i>Omax</i>	ns	ns										
<i>P1</i>	0.10	0.12	ns									
<i>P48</i>	0.20	0.50	ns	0.20								
<i>P50</i>	0.09	0.40	0.07	0.26	0.29							
<i>Pmsy</i>	ns	0.13	ns	ns	0.31	-0.16						
<i>q</i>	-0.69	-0.62	ns	-0.25	-0.44	ns	-0.14					
<i>qs</i>	-0.68	-0.62	ns	-0.25	-0.44	ns	-0.14	0.99				
<i>w</i>	0.03	ns	ns	ns	-0.05	0.03	ns	-0.05	-0.06			
<i>n</i>	0.29	0.36	ns	0.07	0.29	0.16	0.14	-0.32	-0.32	-0.25		
<i>k</i>	-0.03	-0.04	ns	ns	-0.04	ns	-0.02	0.03	0.03	0.03	-0.08	
<i>t</i>	ns	-0.02	ns	ns	ns	ns	ns	0.05	0.05	ns	-0.09	ns

Table 8. Mean, standard deviation and 25, 50, and 75 percentiles of MCMC samples from the posterior distribution for selected parameters of model 2.

Parameter	Mean	sd	25%	Median	75%
<i>K</i>	811.3	548.8	524.5	660.9	884.2
<i>MSY</i>	109	42.4	88.07	95.75	111.3
<i>Omax</i>	2.998	0.1005	2.93	2.998	3.066
<i>P[1]</i>	0.9218	0.1776	0.7951	0.9034	1.032
<i>P[N+1]</i>	1.527	0.27	1.343	1.487	1.671
<i>P50</i>	4.737	1.268	3.894	4.494	5.31
<i>Bmsy/K</i>	2.233	0.2951	2.002	2.265	2.489
<i>q</i>	0.002402	0.000974	0.001756	0.00242	0.003041
<i>qs</i>	0.5907	0.2439	0.4276	0.5911	0.7499
<i>w</i>	0.08823	0.01653	0.07631	0.08669	0.0983
<i>a</i>	0.06582	0.02624	0.04579	0.06335	0.0827
<i>k</i>	0.1553	0.02639	0.1367	0.1518	0.1699
<i>t</i>	0.2243	0.05458	0.1858	0.2141	0.2527

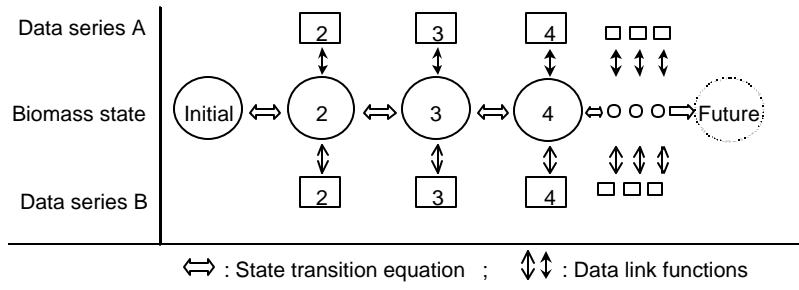


Figure 1. State space model, schematic presentation with two observational series (see text for further explanation).

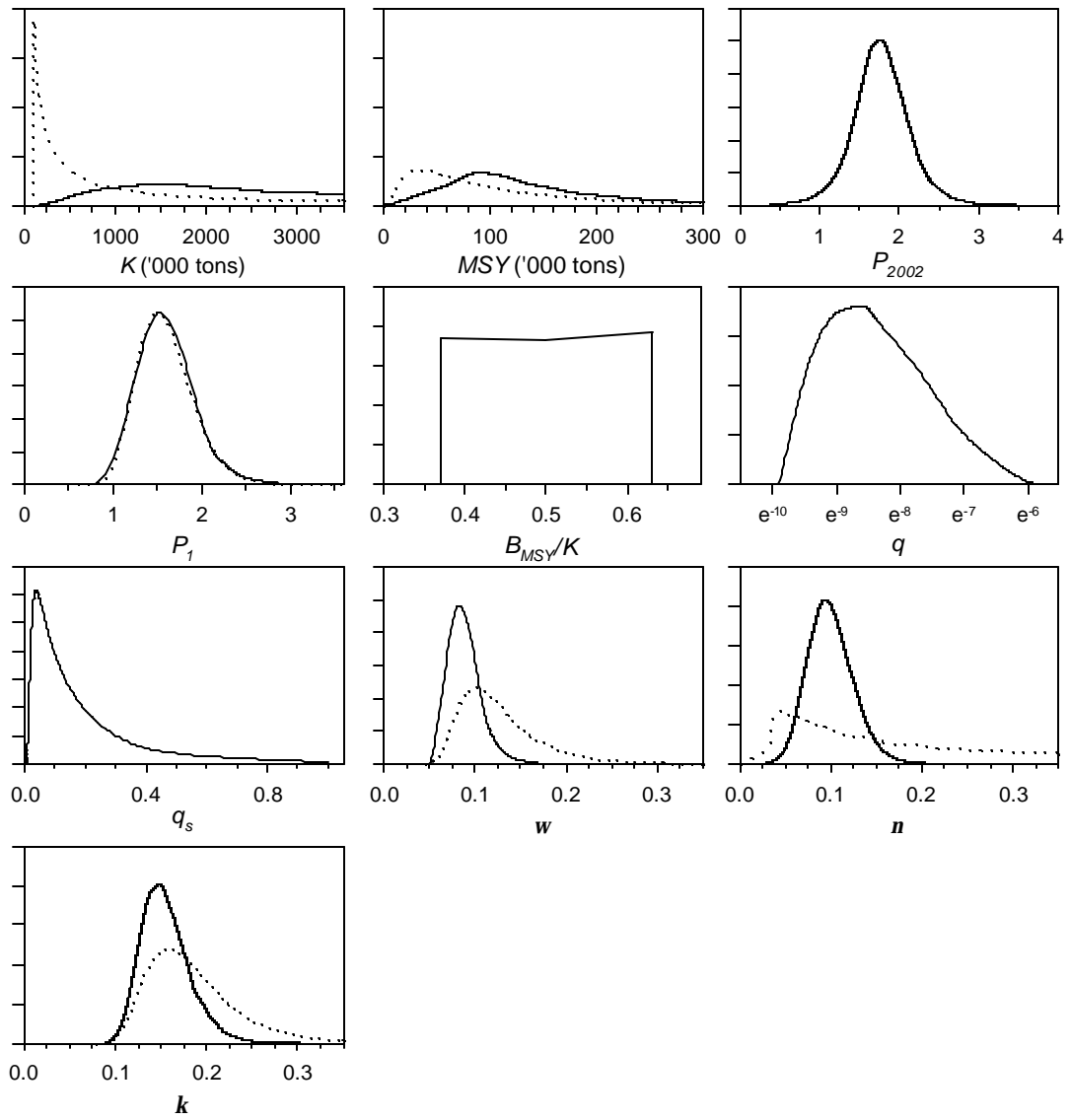


Figure 2. Prior (broken lines) and posterior (solid lines) probability density distributions of the parameters of model 1.

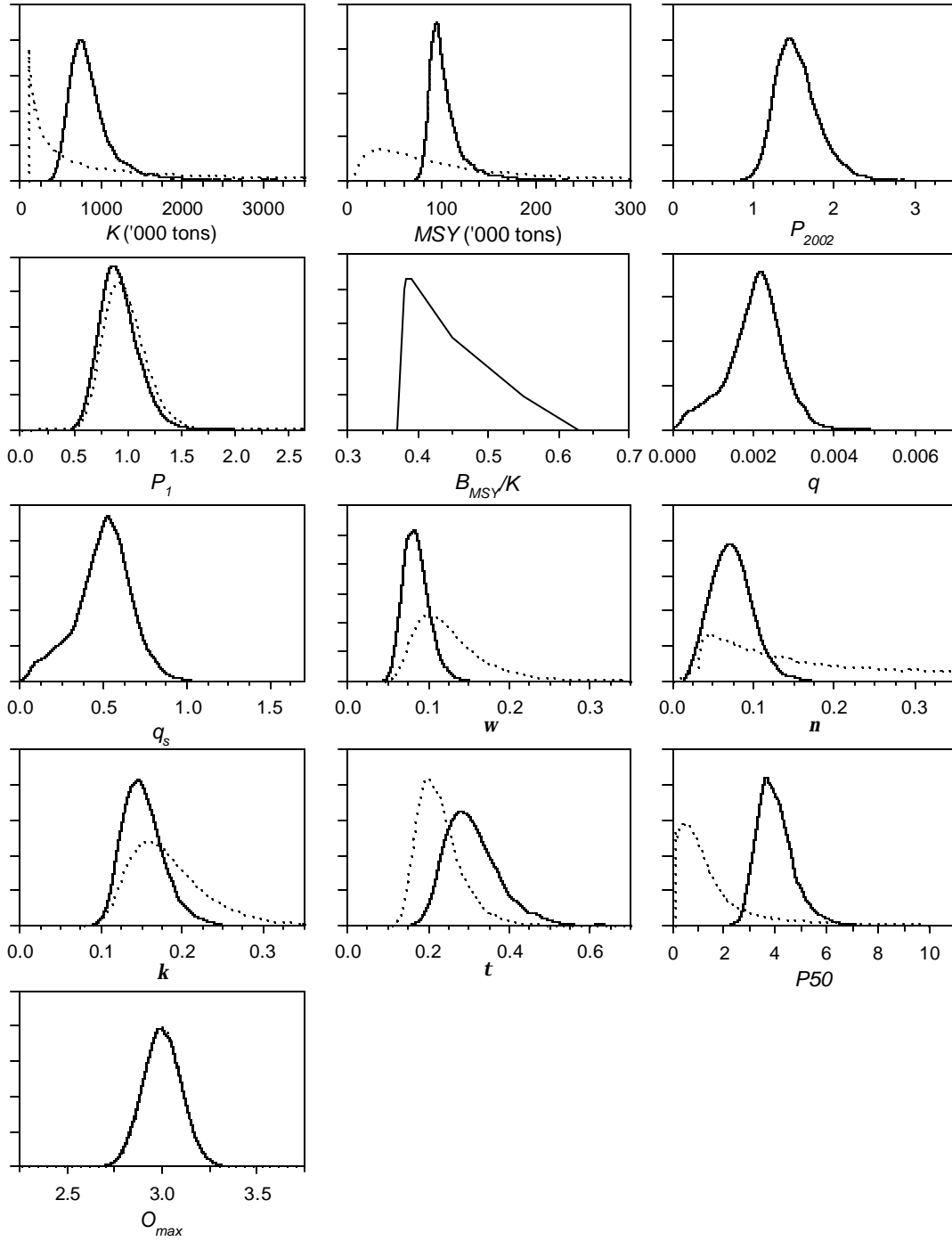


Figure 3. Prior (broken lines) and posterior (solid lines) probability density distributions of the parameters of model 2.

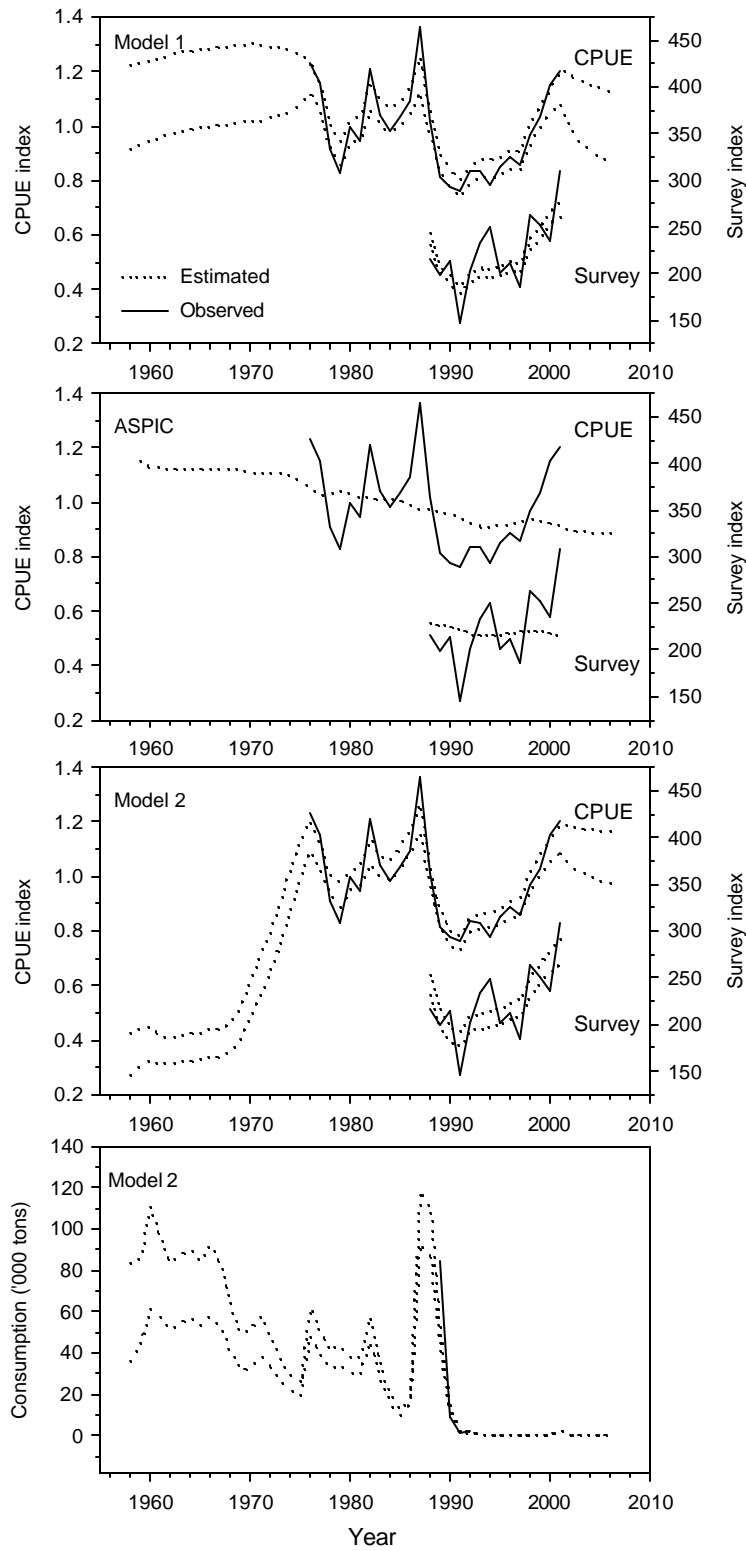


Figure 4. Observed values of biomass indices and consumption and corresponding estimates by model 1 and 2. (25% percentiles of the posteriors) and ASPIC, (least squares estimates). Estimates of relative stock development in the future and historic to the data series are shown in the scale of the CPUE indices.

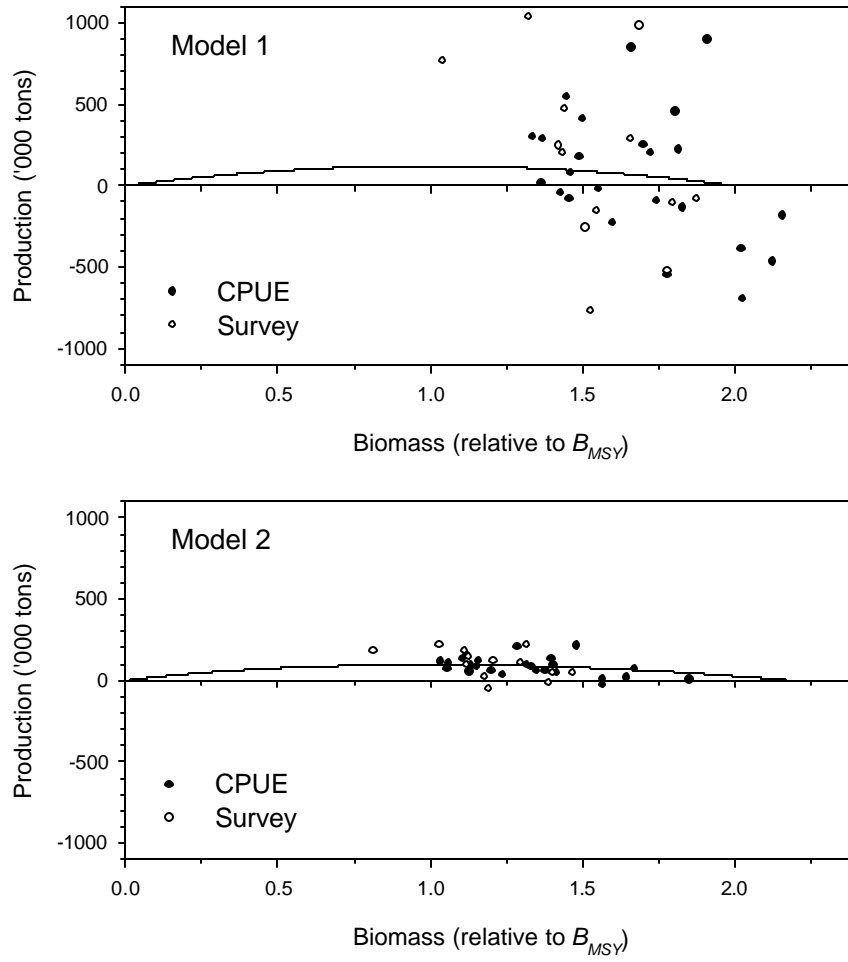


Figure 5. Production vs. stock size as predicted from the indices [more explanation here or in text] and a stock-recruitment curve based on the median of the posteriors of the parameters MSY and m .

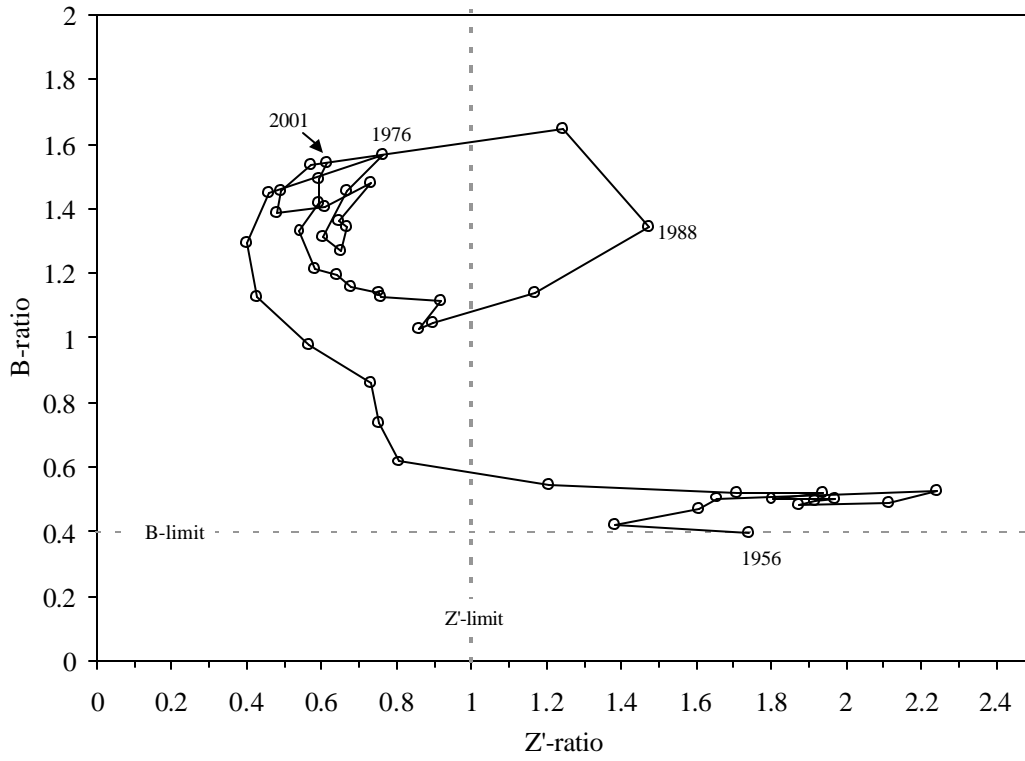


Figure 6. Estimated development of annual median biomass ratio (B/B_{MSY}) and mortality ratio (Z/Z_{MSY}) 1956-2002.