Fitting Bayesian state-space biomass dynamics models to standardized CPUE for carpenter and silver kob stocks

H Winker[1], AJ Booth[2], SE Kerwath[3,1] and CG Attwood[1]

[1]*Zoology Department, University of Cape Town, Private Bag Rondebosch 7700, South Africa.*

[2]*Department of Ichthyology and Fisheries Science, Rhodes University, PO Box 94, Grahamstown 6140, South Africa*

[3]*Marine and Coastal Management, Private Bag X2, Roggebaai 8012, South Africa*

Introduction

The South African boat-based, commercial linefish sector refers to a multi-species, multi-area cluster of low to medium technology boat-based inshore fisheries in which more than 200 fish species are caught manually by hand-lines or rods and reels. Within this cluster one can identify individual fisheries on the basis of fishing strategy, area and target species, but other fisheries such as the demersal trawl fishery also impact on the resource given the considerable overlap in terms of catch compositions (Attwood et al., 2011). The species that account for the largest landings by the linefishery can be roughly grouped into pelagic shoaling species such as yellowtail (*Seriola lalandi*) and snoek (*Thyrsites atun*), demersal species such as silver kob (*Argyrosomus inodorous*) and geelbek (*Atractoscion aequidens*) and reef-associated seabreams including carpenter (*Argyrozona argyrozona*), slinger (*Chrysoblephus puniceus*) and hottentot (*Pachymetopon blochii*).

Monitoring of the linefishery started at the turn of the 20th century with JDF Gilchrist, the Government Marine biologist of the Cape of Good Hope, and the first concerns about overfishing of some linefish species were voiced already in the 1940s (Griffiths 2000). Mandatory catch and effort returns from the boat-based commercial linefishery have been captured since 1985 and stored in the National Marine Linefish System (NMLS), a database hosted by the South African Department of Agriculture, Forestry and Fisheries (DAFF). In 1985, the linefish sector was also formally recognized for the first time and national legislation was introduced to limit effort and fishing mortality. Despite these first regulations, spawner-biomass per-recruit analyses and comparisons with historical catch data in the 1990s indicated alarming states for many linefish stocks (Buxton, 1992; Punt, 1993; Punt et al., 1996; Griffiths, 1997; Griffiths, 2000), which subsequently lead to the declaration of a state of emergency in this fishery in 2000, accompanied by a significant reduction in commercial boat effort (nominally ~ 70%). The forced reduction of effort was reflected in the allocation of medium-term and long-term commercial fishing rights and in the formulation of the linefish management protocol (Griffiths 1997a), which intended to guide the management of stocks according to biological reference points based on spawner biomass per-recruit models.

Several linefish species have been assessed once by spawner-biomass per- recruit analysis. This first wave of assessments was to estimate the relative depletion levels of the stocks, many of which had been exploited for a century by the fishery (Griffiths, 2000). However, there has been no attempt to assess and quantify the impact of the ensuing reduction of commercial effort in 2000, which was designed to rebuild stocks. To date, more than a decade later, there is therefore a pressing need for a new round of linefish assessments. Per-recruit analysis might not be appropriate to quantify a potential recovery of stocks as it relies on the steady-state assumptions of constant fishing mortality and constant recruitment, which will almost certainly be violated in the case of stock rebuilding (Butterworth et al., 1989). Despite catch and effort data being captured since 1985, linefish stock assessment in South Africa has previously been hampered by the inability to standardize the catch-per-unit-effort (CPUE) time series for the effect of multispecies targeting. Recent developments of standardization approaches for multispecies CPUE now permit constructing more reliable time series of abundance indices with potentially useful information for stock assessments (Winker et al., 2012; Winker et al., accepted).

The objective of this study was to assess stock status of carpenter and silver kob twelve years after the emergency in the linefishery. To achieve this, we developed Bayesian state-space biomass dynamic (surplus production) models, which were fitted to time series of landings data and standardized abundance indices. We chose biomass dynamics models because there was insufficient age-disaggregated data available to employ more complex age-structured models. The fairly low data requirements of biomass dynamics models make them an attractive option in situations where reliable information about the size- and age-structure of the stock is difficult to obtain (Hilborn and Walters, 1992). State-space models are regarded as a powerful tool for modelling time-varying abundance indices because they simultaneously account for both process error and observation error (Meyer and Millar, 1999; de Valpine, 2002; Buckland et al., 2004). The process error can account for model structure uncertainty as well as natural variability of stock biomass due to stochasticity in recruitment, natural mortality, growth and maturation, while the observation error determines the uncertainty in the observed abundance index due to reporting error and unaccounted variations in catchability (Meyer and Millar, 1999; Buckland et al., 2004; Ono et al., 2012). A Bayesian framework was chosen to reduce uncertainties about estimates of stock size, fishing mortality and fisheries reference points through the use of informed priors (Punt and Hilborn, 1997; Hilborn and Liermann, 1998; McAllister et al., 2001), which incorporate published literature on historical stock levels and population demographics. The main output of the assessment models are biplots that simultaneously portray the trajectory of the exploited stock against target population size and target harvest rate at Maximum Sustainable Yield (MSY) for the period from 1987 to 2012.

Materials and methods

Data

Catch and effort data for the boat-based South African handline fishery were extracted from the National Marine Linefish System (NMLS) and total landing reported by the inshore trawl fleet were obtained from the Department of Agriculture, Forestry and Fishery (DAFF). The time series considered for the analysis was 1987 – 2011. The catches from both fisheries were aggregated by region assuming that the populations of both species can be split into a southern stock and a south-eastern stock (Fig 1). The magnitude of the carpenter and silver kob catches that are discarded by the inshore trawl fleet has been estimated based on based on on-board observer data collected during the period from 2003 to 2006 (Attwood et al., 2011). To account for discard mortality in the assessment models, the reported trawl landings for carpenter and silver kob were multiplied by the estimated pre-discard to post-discard catch ratios of 2.61 and 1.49, respectively (Attwood et al., 2011).

Standardized CPUE time series (1987-2011) were based on commercial hand-line catch and effort data. The raw data comprised mandatory daily catch returns (kg) per species per boat day as estimated by the skipper, vessel number, crew number, hours on sea, the date and catch location. The reported catch location, initially provided as a shore position and a distance offshore, is referenced to the midpoints of 5 × 5 minute latitude and longitude grid-cells. The CPUE data were standardized by following the standardization approach described for carpenter and silver kob in Winker et al. (in press). This approach involves the application of a Generalized Additive Model framework that was designed to adjust for the effect of different fishing tactics by making use of the information contained in the catch composition. Additional predictor variables included in the model are year, month, latitude (lat) and longitude (long), crew size (crew) and mean hours spent at sea per record (hours). For this analysis, the CPUE records for the southern stock were subset into two regions, south-west and south-central (SC), to reflect the geographical division of the fishery and to account for geographical differences in species composition and targeting (Fig.1).

State-space biomass dynamics model

Three principle classes of non-equilibrium estimation frameworks have been widely used for biomass dynamics models: (1) observation error model, (2) process error models and (3) total error models (Polachek et al., 1993; Punt, 2003). A generic formulation for biomass dynamics models can be written as:

$$B_{t+1} = (B_t + g(B_t \mid \boldsymbol{\theta}) - C_t)\exp(\eta_t)$$

$$I_t = qB_t \exp(\varepsilon_{t,j})$$

where is B_t is the biomass at the start of year t, $g(B_t \mid \boldsymbol{\theta})$ denotes the surplus production as function of B_t and a given vector of parameters $\boldsymbol{\theta}$, C_t is the catch in year t (assumed be known), I_t is the relative index of abundance in year t, q the catchability coefficient scaling the modelled biomass to the abundance index I_t, and η_t is the process error in year t and $\varepsilon_{t,i}$ is the observation error for year t in abundance index, with $\eta_t \sim N(0,\sigma^2)$ and $\varepsilon_{t,i} \sim N(0,\tau_i^2)$, respectively.

Each of the three estimation frameworks represents a special case of the generalized model defined by equations (1) and (2), with $\tau^2 = 0$ in the case of process error models, $\sigma^2 = 0$ in the case of observation error models, and a predefined relationship between σ^2 and τ^2 (i.e. $\sigma^2/\tau^2 = C$) in the case of total error models (Punt, 2003). By contrast, state-space models do not require assumptions about a fixed relationship between σ^2 and τ^2, as they are based on likelihood calculations that can integrate over unknown process errors (Meyer and Millar, 1999; Millar and Meyer, 2000; de Valpine, 2002; Punt, 2003). Most recent advances in random effects modelling now allow for treating the process errors as a vector of unobserved random effects $\boldsymbol{\eta} = \{\eta_1 ... \eta_n\}$ that can be integrated out when estimating the process error variance σ^2 (Fournier et al., 2012; Ono et al., 2012; Pedersen et al., 2012; Thorson et al., 2012). This procedure is implemented in the open source software ADMB-RE (Fournier et al., 2012; http://admb-project.org), which provides a computationally efficient way to implement state-space models (Pedersen et al., 2012).

Here, we develop a numerically integrated Bayesian state-space model according to Meyer and Millar (1999), by using the mixed-effect modelling framework in ADMB-RE (Fournier et al., 2012; Pedersen et al., 2012). The production function is assumed to follow the Schaefer (1954) or logistic form:

$$g(B_t) = rB_t\left(1 - \frac{B_t}{K}\right),$$

where r is the intrinsic rate of population increase and K is the biomass at the carrying capacity.

As the exploitation of many linefish species commenced already in the mid-1800s, it would be unrealistic to assume that the biomass at the start of the time series in 1987 approximates the pristine biomass prior to exploitation K. The initial biomass in the first year of the time series was therefore scaled by introducing the model parameter φ, which is defined by the ratio of the biomass in the first year of the CPUE time series to K, such that:

$$B_1 = \varphi K \exp(\eta_1)$$

$$B_t = \left(B_{t-1} + rB_{t-1}\left(1 - \frac{B_{t-1}}{K}\right) - C_{t-1}\right)\exp(\eta_t) \qquad t = 2, 3, \ldots, n$$

As suggested by Meyer and Millar (1999), we re-parameterized the biomass dynamics model by expressing B_t as proportion of K ($P_t = B_t / K$) to improve the efficiency of the estimation algorithm. The stochastic form of the process equation is then:

$$P_1 = \varphi \exp(\eta_1)$$

$$P_t = \left(P_{t-1} + rP_{t-1}(1 - P_{t-1}) - C_{t-1} / K\right)\exp(\eta_t) \qquad t = 2, 3, \ldots, n$$

and the observation equation is given by:

$$I_t = qKP_t \exp(\tau_t) \qquad t = 1, 2, \ldots, n.$$

Management quantities

A number of management related quantities were derived to assess the status of the carpenter and silver kob stocks. These were (1) Maximum Sustainable Yield (MSY), (2) the harvest rate at MSY (H_{MSY}), (3) the biomass at MSY (B_{MSY}), (4) the depletion as a ratio as biomass in 2012 to K (B_{2012}/K), (5) the relative change in biomass since the forced effort reduction in 2000 (B_{2012}/B_{2000}) and (6) the ratio of harvest rate in 2012 to the harvest rate that produces MSY at B_{MSY} (H_{2012}/H_{MSY}), where MSY = $rK/4$, $\mathrm{B}_{\mathrm{msy}} = K/2$ and $\mathrm{H}_{\mathrm{MSY}} = r/2$. Stock status trajectories over the period of the time series (1987 – 2011) are presented in the form of biplot graphs that plot the ratio B_t/B_{MSY} on the y-axis against the ratio H_t/H_{MSY} on the x-axis, where H_{t} is the predicted harvest rate in year t that is calculated as $H_t = C_t / B_t$.

Bayesian state-space estimation framework

A fully Bayesian biomass dynamics model projected over n years requires a joint probability distribution over all unobservable hyper-parameters $\boldsymbol{\theta} = \left\{K, r, q, \varphi, \sigma^2, \tau^2\right\}$ and the n process errors relating to the unobserved random effects vector $\boldsymbol{\eta} = \{\eta_1 ... \eta_t\}$ (Pedersen et al., 2012), together with all observable data in the form of the relative abundance indices $\mathbf{I} = \{I_1 ... I_n\}$ (Meyer and Millar, 1999). Accordingly, the joint posterior distribution of the Bayesian state-space biomass dynamics model can be conceptually divided into three components: (1) a joint prior distribution, (2) a distribution for the process equation and (3) a distribution for the observation equation. The joint prior distribution on the vector of parameters $\boldsymbol{\theta}$ is given by:

$$p(\boldsymbol{\theta}) = p(K)\,p(r)\,p(q)\,p(\varphi)\,p(\sigma^2)\,p(\tau^2)$$

Assuming multiplicative log-normal errors, the probability distribution for the process equation is of the form:

$$p\left(P_1 \mid \varphi, \sigma^2\right)\prod_{t=2}^{n} p\left(P_t \mid P_{t-1}, K, r, \varphi, \sigma^2\right) = \prod_{t=1}^{n}\left\{\frac{1}{\sqrt{2\pi\sigma^2}}\exp\left(-\frac{\eta_t^2}{2\sigma^2}\right)\right\},$$

and the probability distribution for observation equation, given the unobserved random effects for year *t*, η_t , is:

$$\prod_{t=1}^{n} p(I_t \mid q, K, \tau^2, \eta_t) = \prod_{t=1}^{n}\left\{\frac{1}{\sqrt{2\pi(\xi_{t,i}^2 + \tau_i^2)}}\exp\left(-\frac{\ln(I_t) - \ln(qP_tK))^2}{2(\xi_{t,i}^2 + \tau_i^2)}\right)\right\},$$

where $\xi_{t,i}^2$ is observed variance for year *t* and abundance index I_i, which was calculated from the standard errors of year effects that were predicted from the CPUE standardization model. In this approach, the estimated parameter τ^2 corresponds to the additional temporally-invariant variance in the relative abundance index (Butterworth et al., 1993). According to Bayes' theorem, it follows that joint posterior distribution over all unobservable parameters, given the data and unknown random effects, can be formulated as:

$$\begin{aligned} p(\theta \mid \mathbf{I}, \boldsymbol{\eta}) = {} & p(K)p(r)p(q)p(\varphi)p(\sigma^2)p(\tau_i^2) \\ & \times p(P_1 \mid \varphi, \sigma^2)\prod_{t=1}^{n} p(P_t \mid P_{t-1}, K, r, \varphi, \sigma^2) \times \prod_{t=1}^{n} p(I_t \mid, q, K, \tau_i^2, \eta_t) \end{aligned}.$$

Formulation of prior distributions

The formulation of informative prior distributions permits the integration of existent information from literature into the Bayesian estimation framework. In this way, one can, for example, ensure that all possible parameter solutions given the data will be within plausible biological limits of the stock under assessment (McAllister et al., 2001). However, care must be taken not to overstate the precision of priors for uncertain model parameters (Punt and Hilborn, 1997; McAllister et al., 2001). This typically pertains to parameters of absolute biomass (e.g. K), catchability or variance estimates, for which it may not be feasible to objectively specify informative prior distributions given the available information (Punt and Hilborn, 1997; McAllister et al., 2001; Ono et al., 2012).

In this study, we assumed non-informative prior distributions for all model parameters except the intrinsic rate of population increase r and the ratio B_{1987} to K, φ (Table 2). The prior distributions for σ^2, τ^2 and K were chosen to be represented by a reasonably uninformative inverse-gamma distribution:

$$p(x) = \frac{\lambda^k x^{-(k+1)}}{\Gamma(k)} \exp\left(\frac{-\lambda}{x}\right),$$

with the scaling parameters λ and k set to 0.001 (Chaloupka and Balazs, 2007; Zhou et al., 2009; Brodziak and Ishimura, 2012). The choice of this distribution implies that the parameters are approximately uniform on ln(x) (Jeffrey's prior) and has, for example, the property that lower weight is assigned to very higher values of K which assists to prevent implausibly large posterior values of K (McAllister and Kirkwood, 1998). The catchability parameters q are considered to be uniformly distributed (Booth and Quinn II, 2006). As is common practice, a lognormal was chosen to determine informative prior distributions $p(\varphi)$ and $p(r)$ (Meyer and Millar, 1999; McAllister et al., 2001; Brodziak and Ishimura, 2012), such that:

$$p(x) = \frac{1}{\sqrt{2\pi x \sigma_{\ln}}} \exp\left(-\frac{(\ln x - \ln \mu)}{2\sigma_{\ln}^2}\right),$$

where μ denotes prior mean of φ or r and $\sigma_{\ln}$ is the lognormal standard deviation associated with $\ln(\mu)$.

For the base-case scenarios (Model 1), the mean priors for φ were set to $\mu_{\varphi} = 0.15$ and $\mu_{\varphi} = 0.10$ for carpenter and silver kob stocks, respectively. These values are based on the analysis of historical catch and effort records (1897-1906 and 1927-31) in comparison to catch rates for the period 1986-1998 and are generally in agreement with estimated spawner-biomass per-recruit depletion levels (SPR / SPR_0) for both species prior to 2000 (Griffiths, 1997; Brouwer and Griffiths, 2006). To account for the uncertainty around these estimates, we chose a fairly low precision associated with μ_{φ} by setting $\sigma_{\ln}$ to achieve a coefficients of variation (CV) of 40%, so that $\sigma_{\ln}^2 = \ln(\mathrm{CV}^2 + 1)$).

In order to specify a prior distribution for r, we adapted the Leslie matrix method by McAllister et al. (2001). Based on this approach, demographic information can be used to construct an age-structured Leslie matrix $\mathbf{A}$ of the form (Caswell, 2001):

$$\mathbf{A} = \begin{pmatrix} \phi_1 & \phi_2 & \phi_3 & \cdots & \phi_{t_{\max}} \\ S_1 & 0 & 0 & 0 & 0 \\ 0 & S_2 & 0 & 0 & 0 \\ 0 & 0 & \ddots & 0 & 0 \\ 0 & 0 & 0 & 0 & S_{t_{\max}-1} \end{pmatrix} \qquad (14),$$

where ϕ_t is the average number of recruits expected to be produced by an adult female at age t and S_t is the fraction of survivors at age t. Using matrix algebra, the value of r can be approximated from the relationship $\lambda = \exp(r)$, where λ is the dominant eigenvalue of the transition matrix (Quinn and Deriso, 1999; Caswell, 2001). Here, we used the basic matrix analysis tool provided in the Excel add-in 'Poptools' (www.poptools.org) to derive λ from the Leslie matrix, as described in detail by Mollet and Cailliet (2002). The life history parameters used to construct the prior distributions for r were sourced from previous studies on carpenter (Brouwer and Griffiths, 2006) and silver kob (Griffiths, 1997) and are summarized in Table 2.

Age-dependent survival was estimated as $S_t = \exp(-M)$, where M is the instantaneous rate of natural mortality. The average number of recruits expected to be produced by an adult female at age t is expressed as:

$$\phi_t = \alpha W_t \psi_t \tag{15},$$

where α denotes the slope of the origin of the spawner-recruitment relationship (i.e. the ratio of recruits to spawner biomass at very low abundance) (Hilborn and Walters, 1992; Myers et al., 1999; Forrest et al., 2012), W_t is the weight at age t, ψ_t is the fraction of females that are mature at age t. Weight-at-age was estimated as function of the weight to length conversion parameters a and b and length-at-age, L_t, such that $W_t = aL_t^b$. The corresponding L_t for carpenter was calculated based on the Bertalanffy growth function parameters given in Brouwer and Griffiths (2006) (Table 1):

$$L_t = L_\infty(1 - \exp(-k(t - t_0))),$$

while L_t for silver kob growth was calculated using the growth parameters of the Richards function (Schnute, 1981) provided by Griffiths (1997) (Table 1):

$$L_t = L_\infty\left(1 + \frac{\exp(-k(t - t^*))}{p}\right)^{-p} .$$

The fraction of mature females at age t was calculated as a function of:

$$\psi_t = \frac{1}{1+\exp(-(t-t_{m50})/\delta_t)},$$

where t_{m50} is the estimated age-at-50%-maturity (Table 1) and δ_t was set to 0.1 to resemble close to knife-edge maturation. For the calculation of α first consider the Beverton and Holt spawner-recruitment relationship (S-R) of the form:

$$R = \frac{\alpha S}{1+\beta S},$$

where R is the number of recruits, S is the spawner biomass and β is the scaling parameter (Hilborn and Walters, 1992). In contrast to alternative formulations of the Beverton and Holt S-R function, the parameter α can be directly interpreted as the slope in the origin of the S-R curve (Hilborn and Walters, 1992). We re-parameterized α as function of unfished spawner-biomass per recruit SPR_0 and the steepness parameter h of the spawner-recruitment relationship (Myers et al., 1999; Forrest et al., 2012), such that:

$$\alpha = \frac{4h}{(1-h)} SPR_0^{-1},$$

where h is defined as the ratio of recruitment at a spawner biomass that is reduced to 20% of pristine levels to pristine recruitment (Mace and Doonan, 1988), and SPR_0 is a function of:

$$SPR_0 = \left(\sum_{t=1}^{t_{\max}-1} W_t \psi_t \exp(-M) \right) + W_{t_{\max}} \psi_{t_{\max}} \frac{\exp(-Mt_{\max})}{1-\exp(-M)},$$

where the maximum observed age, t_{max}, is treated as a plus group. In contrast to the population-specific parameters α and β, the estimate of the steepness parameter h of the S-R relationship has the advantage that it is directly comparable between populations (Hilborn and Liermann, 1998). This property permits to derive empirical Bayesian priors for h from meta-analyses of multiple stocks (Myers et al., 1999; Dorn, 2002; Forrest et al., 2012). Myers et al. (1999), for example, provided estimates of steepness h for 57 fish species, which they derived from a meta-analysis of spawner-recruitment data for 249 populations. Because there was no specific information on h for silver kob and carpenter available, we adapted a rather generic mean steepness value of h = 0.7 for both species, which represents the overall average steepness value derived for fairly long-lived, highly fecund fishes of medium to large body size (Myers et al., 1999; Rose et al., 2001). Many commercially exploited species, including Sparidae and Scianidae, typically fall into this ecological group of fishes (Winemiller, 1992; Myers et al., 2002), which corresponds to the general domain of periodic life history strategists (Winemiller and Rose, 1992).

Finally, a Monte-Carlo simulation procedure was used to generate prior distributions for r from the Leslie-Matrix (McAllister et al., 2001). For this purpose, random variables of M and h were drawn from a log-normal distribution, with $M = \mu_M \exp(\varepsilon - \sigma_{\ln}^2/2)$, $h = \mu_h \exp(\varepsilon - \sigma_{\ln}^2/2)$ and $\varepsilon \sim N(0, \sigma_{\ln}^2)$. The variance parameters were set to achieve CV's of 20% for both M and h. For each species, we generated a vector 1000 random r deviates. The parameters μ_r and $\sigma_{\ln}^2$, defining the prior distribution for r, were derived by fitting a lognormal distribution to the bootstrap vector. The resultant prior parameter estimates were μ_r = 0.18 and $\sigma_{\ln}^2$ = 0.27^2 for carpenter and μ_r = 0.21 and $\sigma_{\ln}^2$ = 0.26^2 for silver kob (Table 1).

Posterior distributions and uncertainty

Joint posterior probability distributions of model parameters, projections and management quantities were estimated using the Metropolis-Hastings Markov Chain Monte-Carlo (MCMC) algorithm implemented for random effects models in ADMB-RE (Fournier et al., 2012). Convergence of the MCMC chains was diagnosed using the coda package (Plummer et al., 2006) implemented in the statistical software R (R Development Core Team, 2011), adopting minimal thresholds of p = 0.05 for Geweke's diagnostic (Geweke, 1992) and the two-stage Heidelberger-Welch stationary test (Heidelberger and Welch, 1992).

The mixing in the MCMC chains was generally fairly slow and often insufficient. The latter appeared to be caused by non-stationary behaviour of the process error variance σ^2. We therefore introduced a double-logistic function as a penalty to constrain the ratio $V_R = \tau^2/\sigma^2$ within the boundaries by:

$$p = \frac{1}{(1+\exp(-(x-R_1)/\delta_{R1})(1+\exp(-(x-R_2)/\delta_{R2})}\ ,$$

where $R_1 = \hat{V}_R/2$, $R_1 = 2\hat{V}_R$, $\delta_{R1} = 0.02\hat{V}_R$, $\delta_{R1} = 0.04\hat{V}_R$ and $\hat{V}_R$ denotes the ratio unconstrained maximum likelihood estimates $\hat{V}_R = \hat{\tau}^2/\hat{\sigma}^2$. The corresponding negative log-likelihood profile, -ln(p), is illustrated for the example of $\hat{V}_R$ = 4 (Fig. 2). This penalty increased the stability of the MCMC chains substantially and convergence could be achieved for all base-case models after running the MCMC simulation for 2 million cycles, discarding the first 200000 iterations as burn-in phase and then thinning the chain by saving every 200th iteration to reduce autocorrelation.

The 2.5th and 97.5th percentiles of the posterior distributions are used to represent 95% Bayesian credibility intervals for all parameters, projections and management quantities. The estimated 95% credibility intervals are analogous to 95% confidence intervals and can interpreted in the sense that there is a 95% probability that the lower and upper credibility intervals includes the true value given the prior information and the data.

Results and discussion

In 2000, a state of emergency was declared in the South African boat-based handline fishery on the basis of substantially decreased catch rates of important species and alarming results from spawner biomass per-recruit analyses. The emergency was accompanied by a significant reduction in commercial line-boat effort to allow stock recovery. Declines in linefishery catches of carpenter and silver kob were not uniform and generally commenced prior to the forced effort reduction in 2000 and typically reached a minimum during the period 2001 - 2004 (Fig. 3). Inshore trawl catches, by contrast, increased during this period, to the extent that they frequently exceeded the linefishery catches during the first five years after the emergency (Fig. 3).

The model fits appeared to be adequate in that the models were able to predict the observed increase in the standardized CPUE indices. The clearest and most consistent trends were evident for southern-eastern stocks of carpenter (Fig. 4 A) and silver kob (Fig. 4 B), which was supported by fairly narrow 95% credibility intervals. The fit to south coast silver kob data showed moderate departures from the standardized CPUE indices in most recent years (Fig. 4 C).

The posterior medians for the intrinsic rate of population rate *r* were fairly similar for both species but were found to be consistently lower than their corresponding priors means (Tables 1 and 3, Fig. 5). This could indicate a lower stock productivity than predicted by the species' life history traits or perhaps points towards sources of additional fishing mortality that were not accounted for by the available data. On intra-specific comparisons, the posterior medians for *r* were slightly higher for the south-eastern coast stocks.

The models consistently predicted an improvement in biomass compared to levels around 2000, as the drastic management intervention in the linefishery forced harvest rates below those at Maximum Sustainable Yield (Figs. 6 and 7). The two silver kob stocks remain of concern as inshore trawl catches have increased since 2000, slowing down potential recoveries and possibly resulting in growth overfishing due to earlier selectivity.

References

Attwood, C.G., Petersen, S.L., Kerwath, S.E., 2011. Bycatch in South Africa's inshore trawl fishery as determined from observer records. ICES Journal of Marine Science: Journal du Conseil 68, 2163-2174.

Booth, A.J., Quinn II, T.J., 2006. Maximum likelihood and Bayesian approaches to stock assessment when data are questionable. Fisheries Research (Amsterdam) 80, 169-181.

Brodziak, J., Ishimura, G., 2012. Development of Bayesian production models for assessing the North Pacific swordfish population. Fish. Sci. 77, 23-34.

Brouwer, S.L., Griffiths, M.H., 2006. Management of *Argyrozona argyrozona* (Pisces: Sparidae) in South Africa based on per-recruit models. Afr. J. Mar. Sci. 28, 89-98.

Buckland, S.T., Newman, K.B., Thomas, L., Koesters, N.B., 2004. State-space models for the dynamics of wild animal populations. Ecol. Model. 171, 157-175.

Butterworth, D.S., De Oliveira, J.A.A., Cochrane, K.L., 1993. Current initiatives in refining the management procedure for the South African anchovy resource. University of Alaska Fairbanks. Proceedings of the International Symposium on Management Strategies for Exploited Fish Populations., Alaska Sea Grant College Program Report No. 93-02, Fairbanks, Alaska, pp. 439–473.

Butterworth, D.S., Punt, A.E., Borchers, D.L., Pugh, J.B., Hughes, G.S., 1989. A manual of mathematical techniques for linefish assessment. Sancor. South African National Scientific Programmes Report 160, Cape Town, p. 89.

Buxton, C.D., 1992. The application of yield-per-recruit models to two South African sparid reef species, with special consideration to sex change. Fish. Res. 15, 1-16.

Caswell, H., 2001. Matrix population models: Construction, analysis and interpretation. Sinauer Associates, Sunderland, Massachusetts.

Chaloupka, M., Balazs, G., 2007. Using Bayesian state-space modelling to assess the recovery and harvest potential of the Hawaiian green sea turtle stock. Ecol. Model. 205, 93-109.

de Valpine, P., 2002. Review of Methods for Fitting Time-Series Models with Process and Observation Error and Likelihood Calculations for Nonlinear, Non-gaussian State-Space Models. Bull. Mar. Sci. 70, 455-471.

Dorn, M.W., 2002. Advice on West Coast rockfish harvest rates from Bayesian meta-analysis of stock-recruit relationships. N. Am. J. Fish. Manage. 22, 280-300.

Forrest, R.E., McAllister, M.K., Dorn, M.W., Martell, S.J.D., Stanley, R.D., 2012. Hierarchical Bayesian estimation of recruitment parameters and reference points for Pacific rockfishes (*Sebastes* spp.) under alternative assumptions about the stock-recruit function. Canadian Journal of Fisheries & Aquatic Sciences 67, 1611-1634.

Fournier, D.A., Skaug, H.J., Ancheta, J., Ianelli, J., Magnusson, A., Maunder, M.N., Nielsen, A., Sibert, J.R., 2012. AD Model Builder: using automatic differentiation for statistical inference of highly parameterized complex nonlinear models. Optimization Methods and Software 27, 233-249.

Geweke, J., 1992. Evaluating the accuracy of sampling-based approaches to the calculation of posterior moments. In: Berger, J.O., Bernardo, J.M., Dawid, A.P., Smith, A.F.M.s (Eds.), Bayesian Statistics 4: Proceedings of the Fourth Valencia International Meeting. Clarendon Press, Oxford, pp. 169–193.

Griffiths, M.H., 1997. The application of per-recruit models to *Argyrosomus inodorus*, an important South African sciaenid fish. Fish. Res. 30, 103-115.

Griffiths, M.H., 2000. Long-term trends in catch and effort of commercial linefish off South Africa's Cape Province: snapshots of the 20th century South African Journal of Marine Science 22, 81-110.

Heidelberger, P., Welch, P., 1992. Simulation run length control in the presence of an initial transient. Operations Research 31, 1109–1144.

Hilborn, R., Liermann, M., 1998. Standing on the shoulders of giants: learning from experience in fisheries. Rev. Fish Biol. Fish. 8, 273-283.

Hilborn, R., Walters, C.J., 1992. Quantitative fisheries stock assessment: choice, dynamics and uncertainty. Chapman and Hall, New York.

Mace, P.M., Doonan, I.J., 1988. A generalized bioeconomic simulation model for fish population dynamics. New Zealand Fishery Assessment, Research Document, 88/4, p. 51

McAllister, M.K., Kirkwood, G.P., 1998. Bayesian stock assessment: a review and example application using the logistic model. ICES J. Mar. Sci. 55, 1031-1060.

McAllister, M.K., Pikitch, E.K., Babcock, E.A., 2001. Using demographic methods to construct Bayesian priors for the intrinsic rate of increase in the Schaefer model and implications for stock rebuilding. Can. J. Fish. Aquat. Sci. 58, 1871-1890.

Meyer, R., Millar, C.P., 1999. BUGS in Bayesian stock assessments. Can. J. Fish. Aquat. Sci. 56, 1078–1086.

Millar, C.P., Meyer, R., 2000. Non-linear state space modelling of fisheries biomass dynamics Metropolis-Hastings within-Gibbs sampling. Applied Statistics 49, 327-342.

Mollet, H.F., Cailliet, G.M., 2002. Comparative population demography of elasmobranchs using life history tables, Leslie matrices and stage-based matrix models. Marine and Freshwater Research 53, 503-515.

Myers, R.A., Barrowman, N.J., Hilborn, R., Kehler, D.G., 2002. Inferring Bayesian Priors with Limited Direct Data: Applications to Risk Analysis. N. Am. J. Fish. Manage. 22, 351-364.

Myers, R.A., Bowen, K.G., Barrowman, N.J., 1999. Maximum reproductive rate of fish at low population sizes. Can. J. Fish. Aquat. Sci. 56, 2404-2419.

Ono, K., Punt, A.E., Rivot, E., 2012. Model performance analysis for Bayesian biomass dynamics models using bias, precision and reliability metrics. Fish. Res. 125, 173-183.

Pedersen, M.W., Berg, C.W., Thygesen, U.H., Nielsen, A., Madsen, H., 2012. Estimation methods for nonlinear state-space models in ecology. Ecol. Model. 222, 1394-1400.

Plummer, M., Nicky Best, Cowles, K., Vines, K., 2006. CODA: Convergence Diagnosis and Output Analysis for MCMC. R News 6, 7-11

Polachek, T., Hilborn, R., Punt, A.E., 1993. Fitting surplus production models: comparing methods and measuring uncertainty. Can. J. Fish. Aquat. Sci. 50, 2598-2607.

Punt, A.E., 1993. The use of spawner-biomass-per-recruit in the management of linefisheries. Special Publication of the Oceanographic Research Institute, Durban 2, 80-89.

Punt, A.E., 2003. Extending production models to include process error in the population dynamics. Can. J. Fish. Aquat. Sci. 60, 1217-1228.

Punt, A.E., Hilborn, R.A.Y., 1997. Fisheries stock assessment and decision analysis: the Bayesian approach. Rev. Fish Biol. Fish. 7, 35-63.

Punt, A.E., Pulfrich, A., Butterworth, D.S., Penney, A.J., 1996. The effect of hook size on the size-specific selectivity of hottentot *Pachymetopon blochii* (Val.) and on yield per recruit South African Journal of Marine Science 17, 155-172.

Quinn, T.J., Deriso, R.B., 1999. Quantitative fish dynamics. Oxford University Press, New York.

R Development Core Team, 2011. *R*: A language and environment forstatistical computing. R Foundation for Statistical Computing, Vienna.

Rose, K.A., Cowan Jr, J.H., Winemiller, K.O., Myers, R.A., Hilborn, R., 2001. Compensatory density dependence in fish populations: importance, controversy, understanding and prognosis. Fish Fish. 2, 293-327.

Schnute, J., 1981. A versatile growth model with statistically stable parameters. Can. J. Fish. Aquat. Sci. 38, 1128-1140.

Thorson, J.T., Cope, J.M., Branch, T.A., Jensen, O.P., 2012. Spawning biomass reference points for exploited marine fishes, incorporating taxonomic and body size information. Can. J. Fish. Aquat. Sci. 69, 1556-1568.

Winemiller, K.O., 1992. Life history and the effectiveness of sexual selection. Oikos 63, 318-327.

Winemiller, K.O., Rose, K.A., 1992. Patterns of life-history diversification in North American fishes: implications for population regulation. Can. J. Fish. Aquat. Sci. 49, 2196-2218.

Winker, H., Kerwath, S.E., Attwood, C.G., 2012. Report on stock assessments of important South African linefish resources. Report of the Linefish Scientific Working Group, LSWG No. 3, 2012. Department of Agriculture, Forestry and Fisheries, Cape Town, p. 65.

Winker, H., Kerwath, S.E., Attwood, C.G., accepted. Comparison of two approaches to standardize catch-per-unit-effort for targeting behaviour in a multispecies hand-line fishery. Fish. Res.

Zhou, S., Punt, A.E., Deng, R., Dichmont, C.M., Ye, Y., Bishop, J., 2009. Modified hierarchical Bayesian biomass dynamics models for assessment of short-lived invertebrates: a comparison for tropical tiger prawns. Marine and Freshwater Research 60, 1298–1308.

Table 1 Summary of prior probability density functions used to fit Bayesian state-space models to data from carpenter and silver kob stocks

Prior type	Carpenter	Silver Kob
Non-informative	K ~ inversegamma(0.001,0.001)	K ~ inversegamma(0.001,0.001)
Informative	r ~Lognormal(-1.746,0.266)	r ~Lognormal(-1.551,0.258)
Informative	φ ~ Lognormal(-1.897,0.385)	φ ~ Lognormal(-2.659,0.385)
Non-informative	ln(q) ~ Uniform(-10,2)	ln(q) ~ Uniform(-10,2)
Non-informative	σ^2 ~ inversegamma(0.001,0.001)	σ^2 ~ inversegamma(0.001,0.001)
Non-informative	τ^2 ~ inversegamma(0.001,0.001)	τ^2 ~ inversegamma(0.001,0.001)

Table 2 Summary of life history parameters used to derive informative priors for the intrinsic rate of population increase *r*.

Species	Parameter	Value		Source
Carpenter	L_∞	619	mm FL	Brouwer & Griffith (2005)
	k	0.06	year^{-1}	Brouwer & Griffith (2005)
	t_0	-4.5	years	Brouwer & Griffith (2005)
	a	0.00004	g	Brouwer & Griffith (2005)
	b	2.924	g mm^{-1}	Brouwer & Griffith (2005)
	M	0.10	year^{-1}	Brouwer & Griffith (2005)
	t_{m50}	4	years	Brouwer & Griffith (2005)
	δ_t	0.10	year^{-1}	assumed ~ knife-edge
	$t_{\max}$	30	years	Brouwer & Griffith (2005)
Silver Kob	L_∞	1142	mm FL	Griffiths (1997)
	k	0.65	year^{-1}	Griffiths (1997)
	t^*	-4.5	years	Griffiths (1997)
	p	0.26		Griffiths (1997)
	a	0.000006	g	Griffiths (1997)
	b	3.07	g mm^{-1}	Griffiths (1997)
	M	0.15	year^{-1}	Griffiths (1997)
	t_{m50}	2.4	years	Griffiths (1997)
	δ_t	0.10	year^{-1}	assumed ~ knife-edge
	$t_{\max}$	30	years	Griffiths (1997)

Table 3. Posterior means and 95% Bayesian credibility intervals for the southern and south-eastern carpenter and silver kob stocks.

	Carpenter southern stock		Silver kob southern stock	
Parameters	Median	95% Credibility Interval	Median	95% Credibility Interval
K	23335.0	10722.1 - 52505.5	107285.0	45752.2 - 239456.0
r	0.149	0.117 - 0.210	0.097	0.072 - 0.128
φ	0.182	0.085 - 0.351	0.087	0.042 - 0.200
q_{SW}	0.015	0.012 - 0.018	0.006	0.004 - 0.009
q_{SC}	0.020	0.016 - 0.025	0.010	0.007 - 0.014
σ^2	0.00097	0.00039 - 0.00254	0.0010	0.0005 - 0.0021
τ^2_{SW}	0.00556	0.00197 - 0.01353	0.0120	0.0059 - 0.0241
τ^2_{SC}	0.00562	0.00204 - 0.01396	0.0146	0.0086 - 0.0272
MSY	863.2	554.4 - 1644.0	2571.0	1285.1 - 5130.3
H_{MSY}	0.075	0.059 - 0.105	0.048	0.036 - 0.064
B_{MSY}	11667.5	5361.0 - 26252.7	53642.5	22876.1 - 119728.0
B_{2012}/K	0.361	0.173 - 0.644	0.1269	0.0605 - 0.2895
B_{2012}/B_{2000}	2.328	2.02 - 2.69	1.56	1.41 - 1.76
	Carpenter south-eastern stock		Silver kob southern-eastern stock	
Parameters	Median	95% Credibility Interval	Median	95% Credibility Interval
K	23588.8	11922.5 - 50836.0	30543.5	14802.9 - 66970.5
r	0.164	0.121 - 0.211	0.141	0.109 - 0.178
φ	0.120	0.12 - 0.059	0.075	0.075 - 0.036
q_{SE}	0.023	0.013 - 0.031	0.024	0.016 - 0.032
σ^2	0.00208	0.00090 - 0.00481	0.00092	0.00039 - 0.0023
τ^2_{SE}	0.01109	0.00592 - 0.02221	0.00522	0.00244 - 0.0112
MSY	959.8	567.7 - 567.7	1067.1	577.5 - 2123.1
H_{MSY}	0.082	0.060 - 0.105	0.070	0.055 - 0.089
B_{MSY}	11794.4	5961.25 - 25418.0	15271.8	7401.5 - 33485.2
B_{2012}/K	0.394	0.207 - 0.667	0.178	0.085 - 0.349
B_{2012}/B_{2000}	3.440	2.80 - 4.23	2.44	2.10 - 2.86

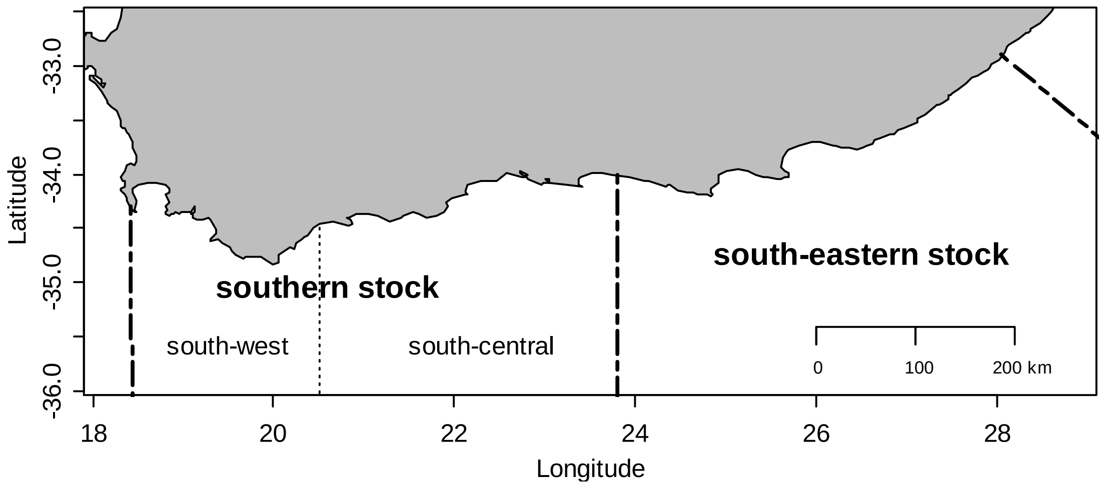

Fig.1 Map showing the regional split for southern and south-eastern stocks of carpenter and silver kob.

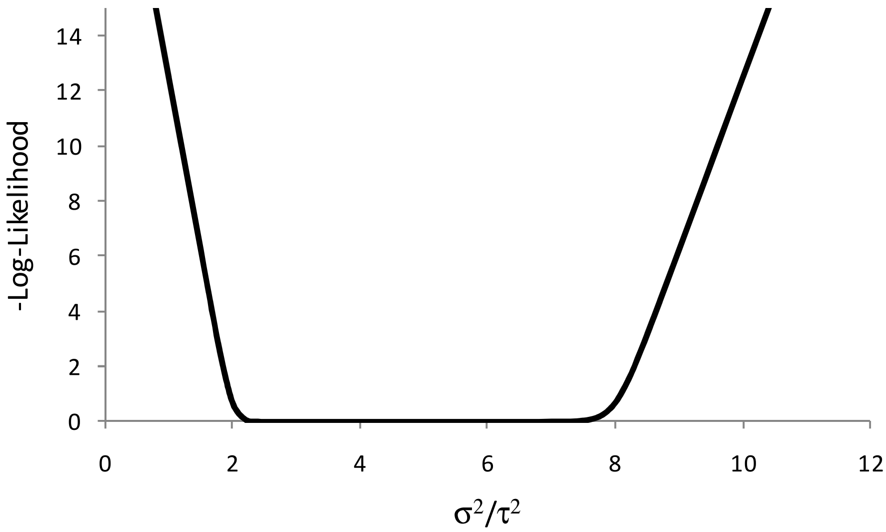

Fig. 2 illustrating a negative log-likelihood profile for used as penalty to stabilize the MCMC runs. The example is based on $\hat{V}_R = \hat{\tau}^2 / \hat{\sigma}^2$ = 4 (see text).

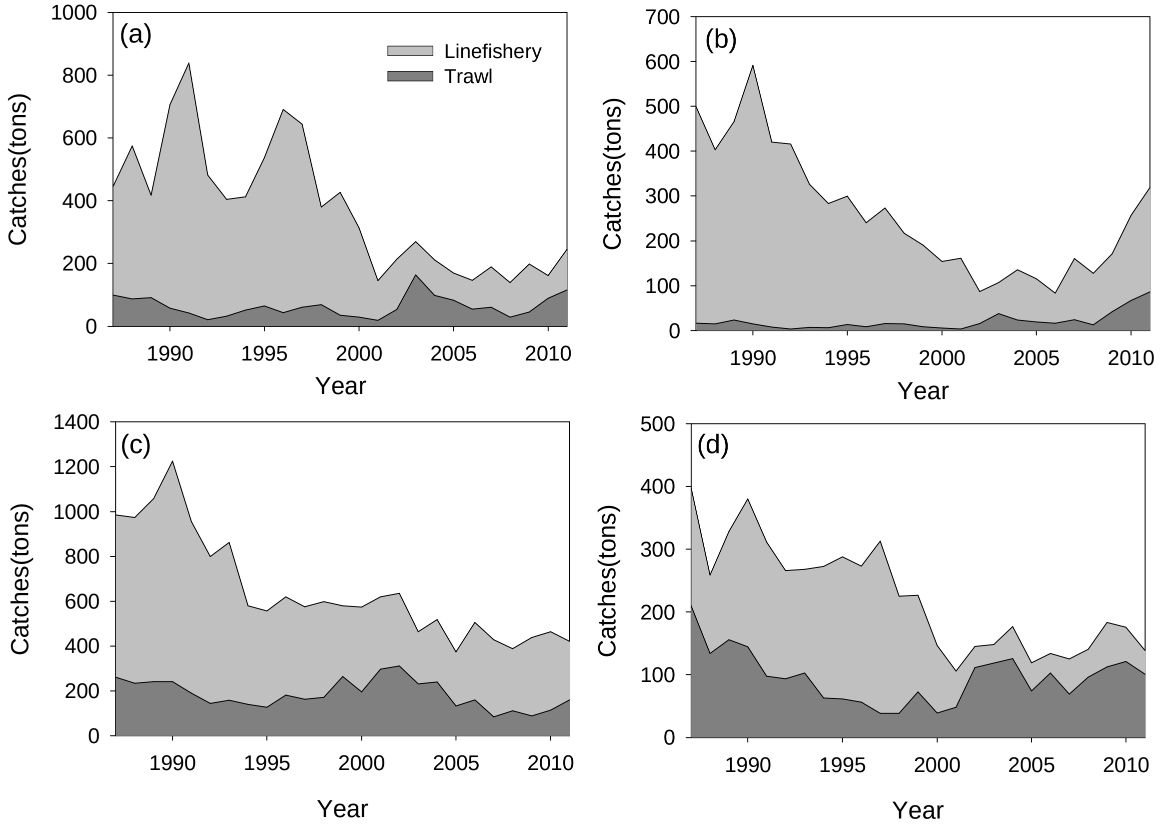

Fig. 3 Cumulative area plots illustrating total catches (tons) by sector for (a) carpenter south, (b) carpenter east, (c) silver kob south and (d) silver kob east

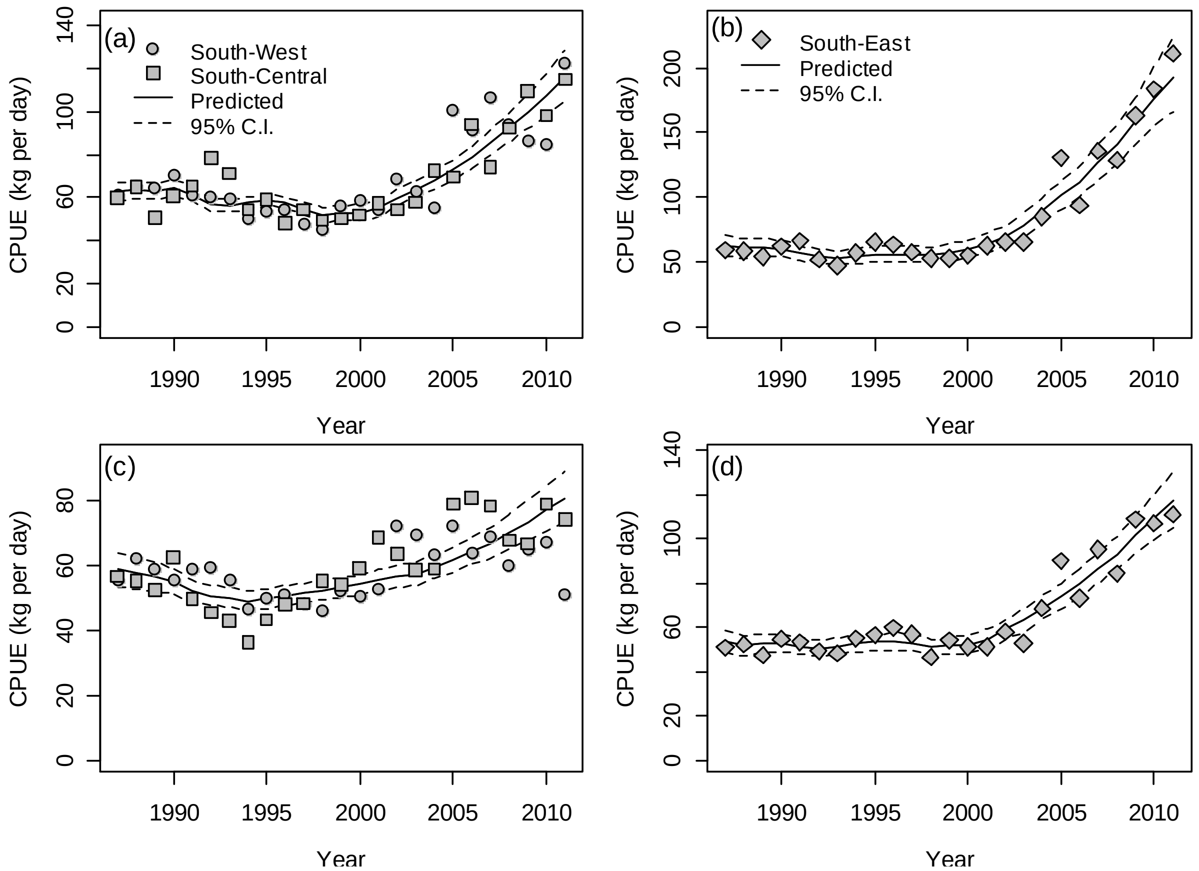

Fig. 4 Standardized CPUE indices and model fits for (a) carpenter south, (b) carpenter south-east, (c) silver kob south and (d) silver kob south-east. Note that the CPUE from the south-central CPUE was scaled to the CPUE from the south-west coast by applying the estimated catchability coefficients.

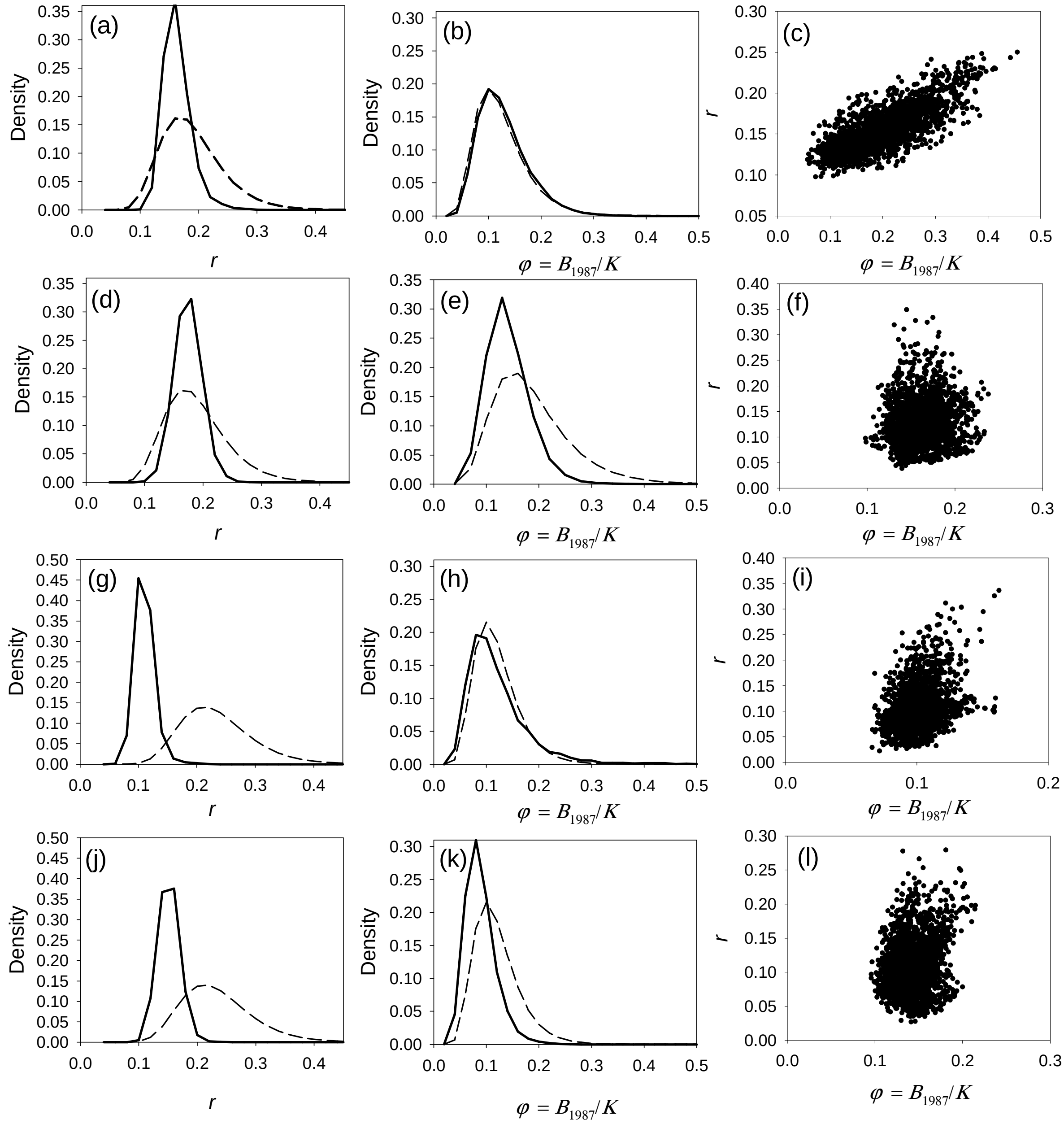

Fig. 5 Informative prior and joint posterior distributions for carpenter south (a) – (c), carpenter south-east (d) – (f), silver kob south (g) – (i) and silver kob south-east (j) – (l).

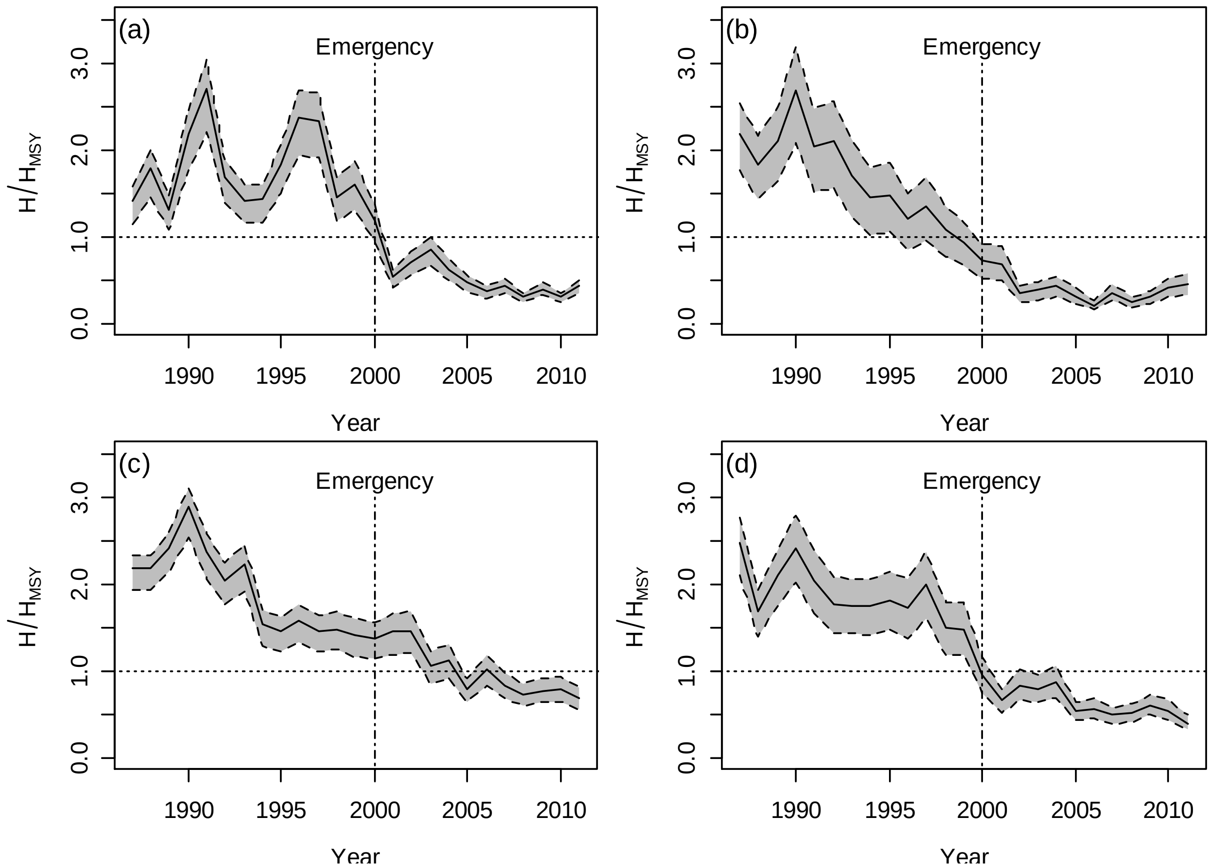

Fig. 6 Ratio harvest rate to HMSY for (a) carpenter south, (b) carpenter south-east, (c) silver kob south and (d) silver kob south-east. The gray shaded areas illustrate the 95% credibility intervals.

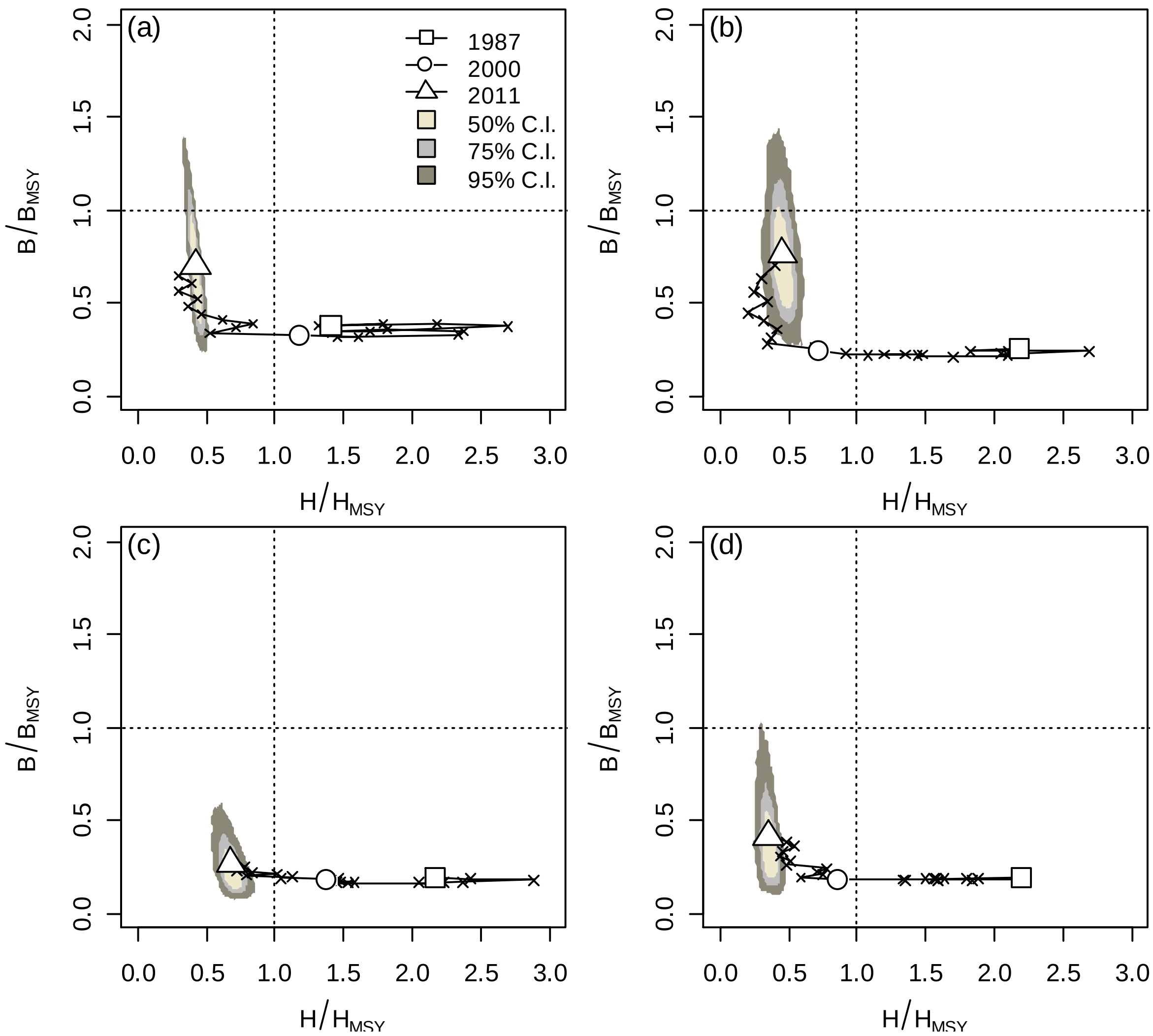

Fig. 7 Biplots illustrating the predicted trajectories of the ratios B/B_{MSY} and H/H_{MSY} for (a) carpenter south, (b) carpenter east, (c) silver kob south and (d) silver kob east. The shaded areas show kernel densities representing the 50%, 75% and 95% credibility intervals.