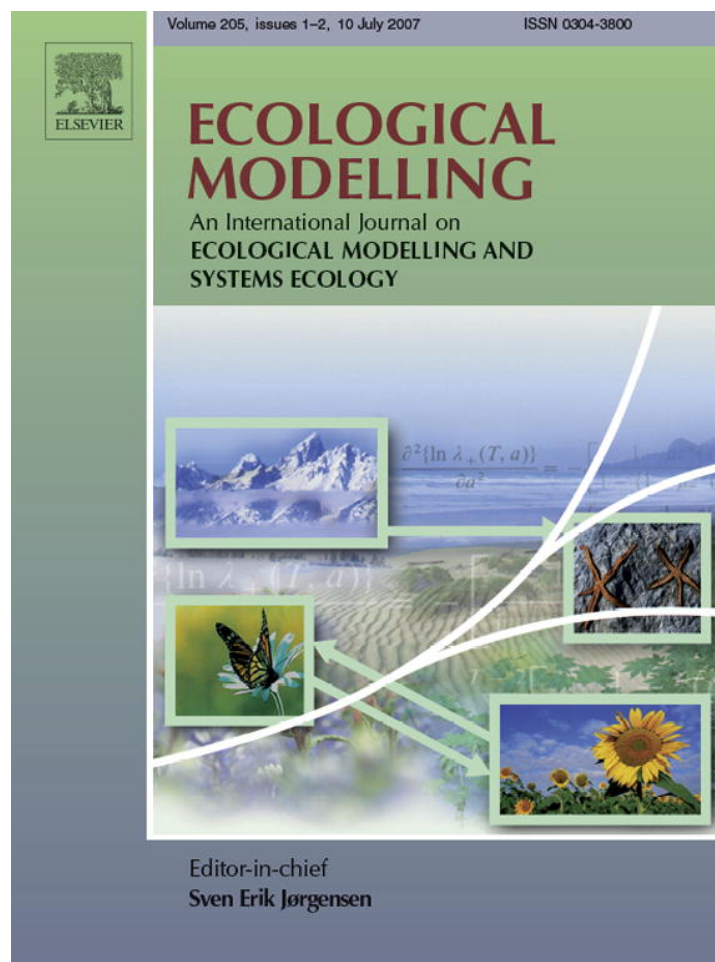


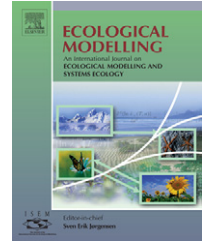
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# Using Bayesian state-space modelling to assess the recovery and harvest potential of the Hawaiian green sea turtle stock

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## ABSTRACT

The Hawaiian green sea turtle genetic stock is endemic to the Hawaiian Archipelago. This stock was depleted over the past century mainly due to over-exploitation that ceased during the 1970s following protection under the US Endangered Species Act. Nesting trends suggest the stock has been recovering but no formal stock assessment has been undertaken. So, we used a Bayesian state-space surplus-production model to describe Hawaiian green turtle population dynamics given limited data and uncertainty about sea turtle demography. Data series comprised commercial landings of green turtles reported from the Archipelago (1944–1973) and nester abundance recorded at the primary rookery on East Island, French Frigate Shoals (1973–2004). The model incorporated process and observation error and was fitted using Markov chain Monte Carlo simulation with a mix of informative and non-informative priors. We estimated that the Hawaiian green turtle stock was ca. 20% of pre-exploitation biomass when monitoring and protection began in the 1970s. The stock is estimated to be now ca. 83% of pre-exploitation biomass with an intrinsic growth rate ca. 5.4% pa (95% Bayesian credible interval: 3.1–8.9%). Rebound or recovery potential (also exploitation rate at MSP) of this stock was estimated to be 3.4% (1.6–6.2%), which is consistent with estimates for other long-lived late-maturing marine species. So, this once-seriously-depleted green turtle stock is well on the way to recovery and a limited harvest might now be demographically feasible. These findings are relevant for supporting informed public policy debate on the restoration of indigenous hunting rights in the Archipelago. Parameter estimates and model structure from the Bayesian surplus-production model were incorporated in an interactive easy-to-use stochastic simulation model to help support policy analysts in stock recovery planning and to explore sustainable harvest potential.

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## 1. Introduction

The green sea turtle, *Chelonia mydas*, is the most abundant large long-lived marine herbivore (Bjorndal, 1997) and has a long history of human exploitation for meat and eggs (Parsons, 1962). The Hawaiian green turtle stock is increasing in abundance following severe depletion due to nesting

habitat destruction (Amerson, 1971) and over-exploitation of eggs and turtles (Balazs and Chaloupka, 2004a). Green turtles resident in Hawaiian waters comprise a single genetic stock (Bowen et al., 1992) that is dispersed over numerous coral reef and coastal foraging grounds throughout the Hawaiian Archipelago (Balazs and Chaloupka, 2004b). Adult female turtles resident in these foraging grounds migrate every few years

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to nest mainly on sand islands at French Frigate Shoals, which is located in the northwest of the Archipelago (Balazs and Chaloupka, 2004a). Nesting habitat in French Frigate Shoals was reduced as a consequence of military activity during the 1930s and then in the late 1940s due to construction and operation of a LORAN surveillance station (Amerson, 1971).

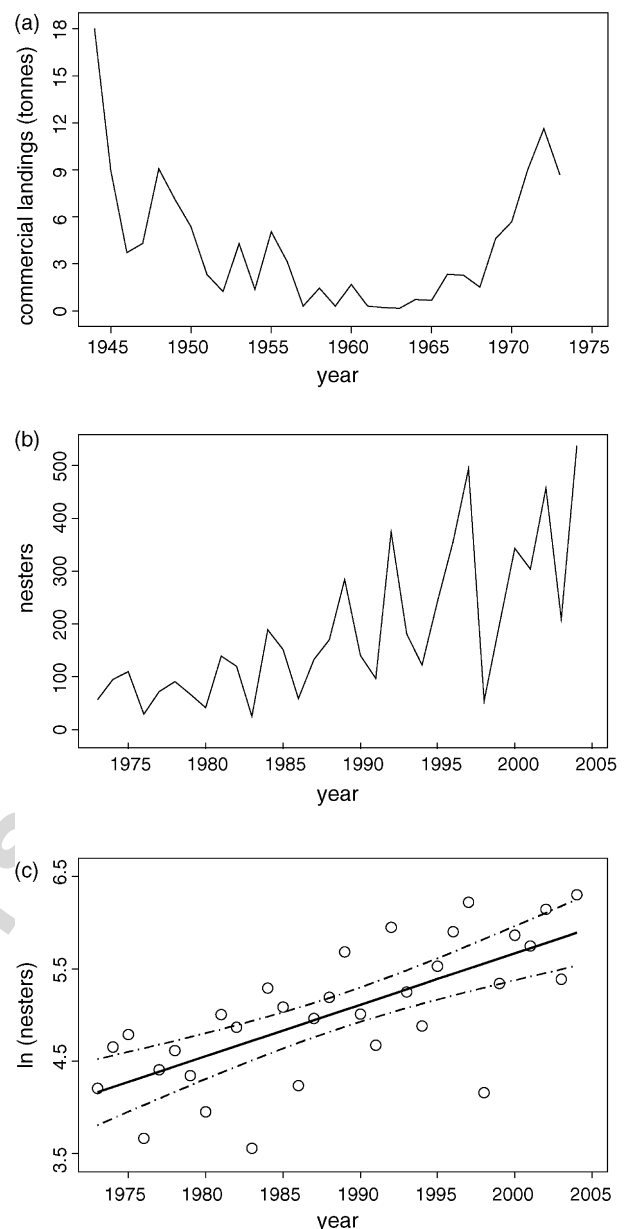
Green turtles, including nesting females, were harvested during exploratory expeditions to the Northwestern Hawaiian Islands in the 19th century (Amerson, 1971). The historical exploitation of green turtles in the Archipelago is poorly documented but may have been quite extensive (Amerson, 1971; Balazs, 1980). The commercial harvest of Hawaiian green turtles developed during the mid-1940s (Amerson, 1971) and increased significantly during the late 1960s and early 1970s (Fig. 1a), which was mainly due to increasing local tourism and restaurant demand (Witzell, 1994). Commercial harvesting ceased in 1974 when the Hawaiian stock was seriously depleted (Balazs and Chaloupka, 2004a). Comprehensive annual surveys of green turtle nesting at the main rookery in French Frigate Shoals have been conducted since 1973 (Balazs and Chaloupka, 2004a). Nesting trends suggest that the stock has been recovering since the late 1970s (Fig. 1b) and there are now increasing demands to delist the species under the US Endangered Species legislation and to consider the restoration of indigenous hunting rights (Kinan and Dalzell, 2005). However, no formal stock assessment of Hawaiian green turtles has been undertaken because of a lack of suitable harvest and demographic information (Balazs and Chaloupka, 2004b).

So, we use a Bayesian state-space modelling approach to fit a stochastic population dynamics model to the Hawaiian green turtle nesting abundance data series given the known commercial harvest history. This Bayesian inference approach enabled prior knowledge of green turtle demography to be incorporated in order to supplement the limited information available for the Hawaiian stock (Chaloupka, 2002, 2004). This approach also enables uncertainty in model parameter estimates and the significant observed temporal variability of the nesting abundance data (Fig. 1b) to be accounted for explicitly. The main objective was to determine whether it was possible to derive meaningful estimates of important population and management parameters for the Hawaiian green turtle stock based on limited data availability. It is anticipated that these estimates could then be used to assess the current recovery status of the Hawaiian green turtle stock and to determine whether a limited harvest for indigenous cultural purposes might be demographically feasible.

## 2. Data and modelling approach

### 2.1. Data series

Data available for stock assessment of the Hawaiian green turtle stock comprise the reported annual landings in the Hawaiian Archipelago  $h_t$ ,  $t = 1944, \dots, 1973$  (Fig. 1a), and a relative abundance index  $I_t$ ,  $t = 1973, \dots, 2004$ , which is the number of female green turtles that nest each year at the stock-specific rookery on East Island, French Frigate Shoals (Fig. 1b). The nesting series was based on the annual rookery



**Fig. 1 – Time series of (a) reported commercial landings from 1944 to 1973 of green sea turtles in the Hawaiian Archipelago and (b) annual number of green turtles recorded nesting at the East Island rookery (French Frigate Shoals) from 1973 to 2004. The underlying trend in annual nester abundance at the East Island rookery is shown in (c) where solid curve shows a generalised smoothing spline fit, dashed curves show 95% Bayesian confidence interval and open dots show the data (note the log scale).**

surveys conducted since 1973 (Balazs and Chaloupka, 2004a). Reported landings or harvest ( $h_t$ ) ceased in 1973 and represents an unknown fraction ( $\gamma$ ) of the true harvest (Balazs, 1980), which is assumed to be  $H_t = \gamma^{-1}h_t$ , where  $\gamma$  is a constant estimable parameter. Age composition data are not available for the harvest series (Balazs, 1980) or for Hawaiian green turtle abundance (Balazs and Chaloupka, 2004b). The trend in the observed nester abundance (Fig. 1b) was estimated using a

generalised smoothing spline regression approach (Gu, 2002), which uses the data to determine the underlying trend without assuming any specific functional form. It is clear from the smoothing spline trend that the Hawaiian green turtle nesting population has increased significantly over the last 25 years or more (Fig. 1c). This smoothing spline trend was then also used to evaluate the fit of the Bayesian state-space model outlined below.

2.2. Bayesian state-space model

Surplus-production models are the most commonly used stock assessment approach when limited to data comprising only harvest and relative abundance time series (Hilborn and Walters, 1992). Hence, the Hawaiian green turtle stock dynamics was accounted for by fitting a surplus-production model using the annual harvest time series and the East Island nesting time series within a Bayesian state-space modelling framework. A state-space model describes the temporal dynamics of two linked processes that may include error in either process: (1) a state process that describes the unobserved population dynamics in terms of biomass or abundance and (2) an observation process based on population-specific survey data that are a function of the unobserved state process (Buckland et al., 2004). Error in the state process is due to demographic variability and is commonly referred to as process error (Punt, 2003). Observation process error can be due to measurement error or because the data display substantial temporal variability (Punt, 2003), like the green turtle nester series that is due to environmental stochasticity (Fig. 1b).

A Bayesian state-space modelling approach (Millar and Meyer, 2000) was then used to fit a stochastic green turtle population dynamics model to the nester series while accounting for process and observation error as well as our prior knowledge about green turtle demography. The Bayesian model comprised the following probability density function (pdf)

$$g_t(B_t|B_{t-1}, \theta) \quad \text{a state process pdf} \quad (1a)$$

$$g_0(B_0, \theta) \quad \text{an initial state pdf} \quad (1b)$$

$$f(I_t|B_t, \theta) \quad \text{an observation process pdf} \quad (1c)$$

where  $B_t$  is the unobserved annual biomass in tonnes for the Hawaiian green sea turtle stock exposed to harvesting ( $t=1944, \dots, 2004$ ),  $I_t$  the observed annual number of green turtles nesting at the East Island rookery ( $t=1973, \dots, 2004$ ), and  $\theta$  is a vector of model parameters. Annual nestings between 1944 and 1972 were then treated as unobserved random variables in the Bayesian modelling framework outlined below.

The state process (1a) was then defined as follows in discrete time form (Hilborn and Walters, 1992):

$$B_t = B_{t-1} + f(B_{t-1}) - H_{t-1} \quad (2)$$

where  $B_t$  is the biomass (tonnes) at beginning of year  $t$  for  $t=1944, \dots, 2004$ ,  $H_t = \gamma^{-1}h_t$  the expected harvest (tonnes) during year  $t$ ,  $h_t$  the reported harvest in tonnes (Fig. 1a),

$\gamma$  the harvest report rate and  $f(\cdot)$  is a surplus-production function specified as the following generalised logistic or Richards-Nelder function (Nelder, 1962):

$$f(B_{t-1}) = rB_{t-1} \left( 1 - \left( \frac{B_{t-1}}{K} \right)^z \right), \quad r > 0, K > 0, z \geq 1 \quad (3)$$

where  $r$  is the intrinsic population growth rate,  $K$  the carrying capacity and the exponent  $z=m-1$  reflects the degree of asymmetry of the production function and so is a measure of density dependence. When  $z=1$  ( $m=2$ ) then (3) is a logistic function otherwise (3) is a skew-asymmetric function. Substituting (3) in (2) provides the biomass dynamics model known in the fisheries literature as a Pella-Tomlinson type surplus-production model (Hilborn and Walters, 1992). This model assumes that it applies to a single closed stock and that the dynamics of the stock are well described by density-dependent growth, mortality and recruitment processes (Zhang et al., 1991). The Hawaiian green turtle stock comprises a single closed genetic stock that is endemic to the Hawaiian Archipelago (Bowen et al., 1992) and various density-dependent processes such as somatic growth and reproduction are apparent for green turtle stocks (Bjorndal et al., 2000; Chaloupka, 2004).

The Pella-Tomlinson type surplus-production model was reparameterised in terms of relative biomass ( $P_t = B_t/K$ ) as follows to reduce parameter confounding such as between biomass and  $K$  that could result in dependent priors (see Meyer and Millar, 1999):

$$P_t = P_{t-1} + rP_{t-1}(1 - P_{t-1}^z) - \frac{H_{t-1}}{K} \quad (4)$$

A number of useful harvest management measures can then be derived from (4) such as BMSP, FMSP, MSP, Bstatus and Fstatus where  $BMSP = K/((z+1)^{1/z})$ ,  $FMSP = r/((z+1)^{1/z})$ ,  $MSP = (BMSP)(FMSP)$ ,  $Bstatus = B_t/BMSP$  and  $Fstatus = F_t/FMSP$  (Zhang et al., 1991). MSP is the maximum surplus-production, BMSP is the biomass at MSP, FMSP is the harvestable fraction at MSP,  $F_t = H_t/B_t$  is the harvested or exploitation fraction where  $H_t = \gamma^{-1}h_t$ . If (4) was a skew-symmetric or logistic surplus-production model with  $z=1$  (or  $m=2$  since  $z=m-1$ ) then  $BMSP = K/2$  and  $FMSP = r/2$  and  $MSP = rK/4$ .

Process error was accounted for in the state process (4) by assuming multiplicative lognormal error as follows for  $t=1945, \dots, 2004$  with diffuse or non-informative priors for the process error variance summarised in Table 1:

$$P_t \sim \text{lognormal}(P_t, \sigma^2) \quad (5)$$

It is common practice in fisheries surplus-production models to assume multiplicative lognormal error for either the state or observation processes (McAllister and Kirkwood, 1998; Punt, 2003). It is also commonly assumed in surplus-production models that the initial biomass ( $B_0$ ) is equal to the carrying capacity ( $K$ ) or that  $P_0 = 1$  (Punt, 2003). However, the Hawaiian green turtle stock was well depleted prior to the reported harvest period shown in Fig. 1a (Balazs, 1980) so that  $B_0 \ll K$  was a more likely but unknown initial state in 1944. Therefore, the initial state process ( $P_{1944} = B_{1944}/K$ ) of the state-

**Table 1 – Summary of prior probability density functions used for the nine parameters in the Bayesian state-space model**

| Parameter                             | Prior                        | Percentiles |                 |       |
|---------------------------------------|------------------------------|-------------|-----------------|-------|
|                                       |                              | 2.5%        | 50%             | 97.5% |
| $r$ (intrinsic growth rate)           | Lognormal( $-2.87, 0.32^2$ ) | 0.03        | 0.06            | 0.11  |
| $K$ (carrying capacity)               | Lognormal( $7.25, 0.75^2$ )  | 542         | 1408            | 3676  |
| $z$ (shape parameter)                 | Uniform(1, 5)                |             | Non-informative |       |
| $q$ (abundance index scale)           | Inverse-gamma(0.001, 0.001)  |             | Non-informative |       |
| $\sigma^2$ (process error variance)   | Inverse-gamma(0.001, 0.001)  |             | Non-informative |       |
| $\tau^2$ (observation error variance) | Inverse-gamma(0.001, 0.001)  |             | Non-informative |       |
| $\gamma$ (harvest report rate)        | Beta( $\alpha, \beta$ )      |             |                 |       |
| $\alpha$ (report rate hyperprior)     | Uniform(1, 100)              |             | Non-informative |       |
| $\beta$ (report rate hyperprior)      | Uniform(1, 100)              |             | Non-informative |       |

space model (1b) was sampled from a uniform prior pdf to reflect non-informative and uncertain initial relative biomass in 1944 at the start of the reported harvest time series (Fig. 1a):

$$P_{1944} \sim \text{uniform}(0.01, 3) \quad (6)$$

The observation process of the model (1c) assumes that the relative abundance index ( $I_t$ ; Fig. 1b) is proportional to the relative biomass ( $P_t$ ) as follows (Meyer and Millar, 1999):

$$I_t = qKP_t \quad (7)$$

where  $q$  is the relative abundance scaling factor also known as the catchability coefficient in the fisheries literature (Hilborn and Walters, 1992). Observation error was also accounted for in the observation process (7) as follows for  $t=1944, \dots, 2004$  with non-informative priors for the observation error variance summarised in Table 1:

$$I_t \sim \text{lognormal}(I_t, \tau^2) \quad (8)$$

The Bayesian state-space model (1) then comprises the Pella–Tomlinson type surplus-production state process pdf (4), the initial state pdf (6), the observation process pdf (8) with parameter set  $\Theta = \{r, K, z, q, \sigma^2, \tau^2, \gamma, \alpha, \beta\}$  and the priors listed in Table 1. Besides the parameter set  $\Theta$ , the unobserved variables in (1) included ( $P_{1944}, \dots, P_{2004}$ ), and ( $I_{1944}, \dots, I_{1972}$ ).

The priors comprised informative and non-informative independent priors (Table 1). Non-informative priors were based on recommendations in McAllister and Kirkwood (1998) and Millar and Meyer (2000). The informative prior for population growth rate ( $r$ ) was based on estimates derived from analyses of other green turtle nester trends (Chaloupka and Limpus, 2001; Balazs and Chaloupka, 2004a). The carrying capacity ( $K$ ) prior was based on simulation experiments with (i) a stochastic age-, sex- and spatially structured model (Chaloupka and Balazs, unpublished) to determine the approximate Hawaiian stock size needed to realise the East Island rookery nesting abundance (Fig. 1b) and (ii) stochastic metapopulation models for other green turtle stocks to derive estimates of stable age structure and proportion of mature females in a population like the southern Great Barrier Reef stock (Chaloupka, 2002, 2004). A  $U[0.01, 3]$  prior was used for unknown initial relative biomass (6) to reflect a complete lack of information for the state of this variable at the start of the harvest record in 1944 (Fig. 1a). We could have used an infor-

mative prior for observation error based on an estimate of the temporal variability in nester trends for other green turtle populations but we choose to use as many non-informative priors as possible.

Meyer and Millar (1999) and Rivot et al. (2004) have shown how Bayesian non-linear state-space models can be readily fitted using Markov chain Monte Carlo simulation in WinBUGS (Lunn et al., 2000). We fitted Bayesian state-space model (1) using the WinBUGS code shown in Appendix A based on the Meyer and Millar (1999) BUGS code. Marginal posterior distributions of model parameters, management measures and unobserved variables were based on 250,000 iterations after discarding the first 50,000 iterations (burn-in sample) to ensure no persistent initial pathologic behaviour. These iterations were reduced to 10,000 by sampling every 25th value to avoid sample correlation. The posterior densities were summarised using local likelihood density estimation (Loader, 1999). Model sensitivity to informative priors was then evaluated by using alternative forms of the carrying capacity prior (McAllister and Kirkwood, 1998; Millar and Meyer, 2000). The comparative model fit was evaluated using the deviance information criterion (DIC) developed for Bayesian models (Spiegelhalter et al., 2002) although other approaches are emerging (Aitken et al., 2005). Model convergence diagnostics were performed on two separately initialised chains using the BOA package for R (Smith, 2004).

### 2.3. Stochastic simulation model

The Bayesian state-space model (1) can be used to evaluate various management scenarios by projecting the state process beyond  $t=2004$  following some model-based management intervention. We did this to evaluate constant-offtake harvest scenarios (see Hilborn and Walters, 1992). However, it is easier to use a fast and interactive stochastic simulation model that captures the same structure and estimated parameters of model (1). This sort of model is better suited for supporting scenario and consensus building tasks by interdisciplinary policy or recovery planning teams with little or no modelling background (Ruth and Lindholm, 1996). However, the stochastic simulation model cannot be used to statistically fit the model to the data unlike the state-space model. Hence, the two models together provide a useful ensemble tool for stock recovery or policy planning based on robust estimation given data uncertainty. Therefore, a differential equation based simulation model version of the Bayesian state-space

model (1) was developed. The differential equation form of the Pella–Tomlinson type surplus-production in biomass terms is:

$$\frac{dB}{dt} = rB_{t-1} \left( 1 - \left( \frac{B_{t-1}}{K} \right)^z \right) - H_{t-1} \quad (9)$$

The stochastic surplus-production simulation model comprising state process (9) with lognormal process error and stochastic observation process (8) was then implemented using MADONNA, which is a fast and an easy-to-use ordinary differential equation solver and C-preprocessor (Macey et al., 2000). This model included the harvest and nester series (Fig. 1) and posterior median parameter (or hyperparameter) estimates derived from the Bayesian model. Annotated model code is shown in Appendix B where the lognormal, gamma and beta sampling functions were derived using algorithms in Naylor et al. (1966) since these are not available in MADONNA. All the model parameters are readily changed using interactive parameter devices available in MADONNA to enable the user to easily and quickly explore the model dynamics and to implement different management settings (see Ruth and Lindholm, 1996 for an example addressing multispecies fisheries management).

### 3. Results

#### 3.1. Model summaries

Four variants of the Bayesian state-space surplus-production model were compared: (1) a Pella–Tomlinson surplus-production model with an informative lognormal prior on  $K$ , (2) a logistic surplus-production model ( $z = 1$ ) with all other settings the same as for the previous model, (3) an alternative Pella–Tomlinson surplus-production model with a diffuse uniform prior on  $\log K$  and (4) another alternative Pella–Tomlinson surplus-production model with informative priors on  $K$  and the harvest report rate. The four models were used to help evaluate model sensitivity to informative priors and to the surplus-production functional form. The posterior marginal distributions of all the parameters, stock status indicated by the unobserved variables ( $P_{1944}, \dots, P_{2004}$ ), and ( $I_{1944}, \dots, I_{1972}$ ) and derived management measures for these four models are summarised in Table 2. The posterior mean and median were dissimilar for most parameters, management measures and unobserved variables (Table 2). The means were generally greater than the medians because most distributions were right skewed so that posterior distributions were better summarised by the percentiles (2.5th, 50th = median, 97.5th).

The best-fit of the four models was Model 1 (Table 2a) and it passed all convergence and stationarity diagnostics for the two chains used. While Model 1 was the best-fit model, there was no meaningful difference between all four models based on the DIC since the DIC range was  $<2$  (Table 2). Therefore, the posterior distribution summaries for all four models are given in Table 2 since any of these models could be used for evaluating management interventions given the available data and significant model uncertainty. However, there were major differences in some of the parameters, stock status and management measures for the four models. For instance, the

logistic surplus-production model (Table 2b) estimated that the Hawaiian green turtle stock had recovered to ca. 73% of the pre-exploitation biomass by 2004 compared to ca. 83–90% for the Pella–Tomlinson models (Table 2). Moreover, the logistic and Pella–Tomlinson model with an uninformative carrying capacity prior provide comparatively lower management measures such as MSP and BMSP than the Pella–Tomlinson models with informative priors. These more conservative measures might be more appealing to risk-averse managers. On the other hand, all models estimated that the stock had declined to ca. 21–26% of the pre-exploitation biomass when commercial harvesting of Hawaiian green turtles ceased in 1973.

The three Pella–Tomlinson models (Table 2a, c, d) were slightly better fits than the logistic model ( $z = 1$ ) based on DIC but the precision of the Pella–Tomlinson shape parameter ( $z > 1$ ) was imprecise in all cases despite being significantly  $>1$  (Table 2). So while a skew-asymmetric surplus-production function was evident for the Hawaiian stock there was significant uncertainty about the specific shape of the production function. Furthermore, using an informative prior on the harvest report rate ( $\gamma$ ) also had little effect on model fit or the posterior median of most parameters, management measures or unobservables (cf. Table 2a, d). So while there is no doubt that there was under-reporting of Hawaiian turtle landings (Balazs, 1980; Witzell, 1994), the data were not strongly informative, with all three models with a non-informative report rate prior suggesting that  $\gamma \leq 53\%$  (Table 2a–c). Nonetheless, exploring further, it was found that  $\gamma \leq 35\%$  when using a more informative prior, which imposed a belief that the report rate was  $\ll 50\%$  (Table 2d). So a constant annual report rate ca. 35% might be a better estimate but again the estimate is imprecise (95% credible interval: 9–69%: Table 2d) and fitted no better than Model 1.

#### 3.2. Model trends

The posterior median relative biomass trends for the three models with uninformative harvest rate prior (Table 2a–c) are shown in Fig. 2a. There was little difference in the estimated historical trends from 1944 to 2004 for the logistic and the Pella–Tomlinson model with informative  $K$  prior, although the annual estimates were imprecise (Table 2; see Fig. 2b). The relative biomass trend for the model with an uninformative prior was different from these two models prior to 1973, suggesting that the Hawaiian green turtle stock was not significantly depleted in 1944 at the start of the commercial landings series—perhaps only to ca. 61% of the pre-exploitation biomass (Table 2c). On the other hand, the two models with informative  $K$  prior suggest that the stock was significantly depleted in 1944 to  $<33\%$  of the pre-exploitation biomass. All three models were similar from 1973 onwards when harvesting ceased and population monitoring commenced (Fig. 2a), which suggests that the data are quite uninformative about the historical trend prior to 1973 unless an informative carrying capacity prior was used. The posterior median biomass trends for these models are shown in Fig. 2c where all models suggest the exploitable stock biomass was ca. 300–400 tonnes in 1944, although again the annual biomass estimates were imprecise (Fig. 2d). The predicted posterior median nester trends for the three models with uninformative harvest rate

**Table 2 – Summary of posterior means and percentiles for management parameters and model variables derived from 4 Bayesian state-space surplus-production models**

| Parameter  | Mean   | S.D.   | Percentiles |        |        |
|--|--------|--------|-------------|--------|--------|
|  |        |        | 2.5%        | Median | 97.5%  |
| (a) Model 1 (production function shape parameter $z > 1$ , lognormal prior on $K$ ); DIC = 379.1   |        |        |             |        |        |
| Carrying capacity ( $K$ , tonnes)  | 1863.0 | 1456.0 | 321.1       | 1431.0 | 5835.0 |
| Intrinsic population growth rate ( $r$ )   | 0.056  | 0.015  | 0.031       | 0.054  | 0.089  |
| Abundance index scaling factor ( $q$ )   | 0.512  | 0.739  | 0.050       | 0.287  | 2.453  |
| Production function shape parameter ( $z$ )  | 2.97   | 1.18   | 1.09        | 2.94   | 4.91   |
| Biomass in 1944 (tonnes)   | 906.7  | 1499.0 | 96.7        | 329.0  | 5148.0 |
| Biomass in 1973 (tonnes)   | 437.4  | 523.0  | 43.5        | 278.8  | 1759.0 |
| Biomass in 2004 (tonnes)   | 1548.0 | 1598.0 | 134.1       | 1073.0 | 5846.0 |
| Biomass fraction of $K$ in 1944 ( $P_t = B_t/K$ )  | 0.574  | 0.616  | 0.042       | 0.269  | 1.964  |
| Biomass fraction of $K$ in 1973  | 0.245  | 0.163  | 0.036       | 0.212  | 0.657  |
| Biomass fraction of $K$ in 2004  | 0.843  | 0.445  | 0.131       | 0.834  | 1.850  |
| MSP (maximum surplus-production, tonnes)   | 41.23  | 29.02  | 2.57        | 30.40  | 251.85 |
| Bmsp (biomass at MSP, tonnes)  | 1171.1 | 752.2  | 163.3       | 897.6  | 4063.5 |
| Fmsp (harvestable fraction at MSP)   | 0.035  | 0.008  | 0.016       | 0.034  | 0.062  |
| Fraction of harvest reported ( $\gamma = \text{beta}(\alpha, \beta)$ )   | 0.507  | 0.228  | 0.076       | 0.506  | 0.942  |
| $\alpha$ hyperparameter for harvest report rate beta pdf   | 51.55  | 28.24  | 4.61        | 51.85  | 97.31  |
| $\beta$ hyperparameter for harvest report rate beta pdf  | 50.48  | 28.36  | 3.56        | 50.34  | 97.24  |
| Process error variance ( $\sigma^2$ )  | 0.019  | 0.031  | 0.001       | 0.008  | 0.101  |
| Observation error variance ( $\tau^2$ )  | 0.308  | 0.094  | 0.174       | 0.293  | 0.533  |
| (b) Model 2 (production function shape parameter $z = 1$ , lognormal prior on $K$ ); DIC = 380.9   |        |        |             |        |        |
| Carrying capacity ( $K$ , tonnes)  | 1779.0 | 1410.0 | 329.7       | 1365.0 | 5744.0 |
| Intrinsic population growth rate ( $r$ )   | 0.059  | 0.017  | 0.032       | 0.058  | 0.099  |
| Abundance index scaling factor ( $q$ )   | 0.636  | 0.935  | 0.045       | 0.333  | 2.998  |
| Biomass in 1944 (tonnes)   | 838.9  | 1273.0 | 95.4        | 371.3  | 4377.0 |
| Biomass in 1973 (tonnes)   | 448.8  | 569.1  | 37.1        | 261.5  | 2008.0 |
| Biomass in 2004 (tonnes)   | 1532.0 | 1890.0 | 106.3       | 902.8  | 6855.0 |
| Biomass fraction of $K$ in 1944 ( $P_t = B_t/K$ )  | 0.566  | 0.569  | 0.045       | 0.319  | 1.981  |
| Biomass fraction of $K$ in 1973  | 0.262  | 0.201  | 0.032       | 0.212  | 0.773  |
| Biomass fraction of $K$ in 2004  | 0.865  | 0.653  | 0.096       | 0.727  | 2.472  |
| MSP (maximum surplus-production, tonnes)   | 26.26  | 22.60  | 4.36        | 19.44  | 89.01  |
| Bmsp (biomass at MSP, tonnes)  | 889.7  | 704.9  | 164.9       | 682.7  | 2872.0 |
| Fmsp (harvestable fraction at MSP)   | 0.029  | 0.009  | 0.016       | 0.029  | 0.049  |
| Fraction of harvest reported ( $\gamma = \text{beta}(\alpha, \beta)$ )   | 0.496  | 0.237  | 0.068       | 0.497  | 0.942  |
| $\alpha$ hyperparameter for harvest report rate beta pdf   | 50.17  | 28.64  | 3.88        | 49.82  | 97.37  |
| $\beta$ hyperparameter for harvest report rate beta pdf  | 50.89  | 28.66  | 3.69        | 51.13  | 97.30  |
| Process error variance ( $\sigma^2$ )  | 0.019  | 0.030  | 0.001       | 0.009  | 0.096  |
| Observation error variance ( $\tau^2$ )  | 0.311  | 0.093  | 0.176       | 0.295  | 0.538  |
| (c) Model 3 (production function shape parameter $z > 1$ , uniform prior on $\log K$ ); DIC = 379.7  |        |        |             |        |        |
| Carrying capacity ( $K$ , tonnes)  | 2096.0 | 2523.0 | 93.3        | 837.4  | 8839.0 |
| Intrinsic population growth rate ( $r$ )   | 0.057  | 0.016  | 0.031       | 0.055  | 0.092  |
| Abundance index scaling factor ( $q$ )   | 1.144  | 1.786  | 0.029       | 0.471  | 6.456  |
| Production function shape parameter ( $z$ )  | 2.86   | 1.16   | 1.08        | 2.76   | 4.89   |
| Biomass in 1944 (tonnes)   | 1022.0 | 2222.0 | 90.71       | 300.8  | 8261.0 |
| Biomass in 1973 (tonnes)   | 556.0  | 855.6  | 22.05       | 185.1  | 2840.0 |
| Biomass in 2004 (tonnes)   | 1950.0 | 2757.0 | 49.36       | 632.2  | 9554.0 |
| Biomass fraction of $K$ in 1944 ( $P_t = B_t/K$ )  | 0.765  | 0.633  | 0.043       | 0.609  | 1.997  |
| Biomass fraction of $K$ in 1973  | 0.287  | 0.156  | 0.039       | 0.264  | 0.674  |
| Biomass fraction of $K$ in 2004  | 0.907  | 0.421  | 0.155       | 0.897  | 1.890  |
| MSP (maximum surplus-production, tonnes)   | 46.46  | 37.39  | 0.75        | 17.64  | 393.75 |
| Bmsp (biomass at MSP, tonnes)  | 1307.1 | 198.96 | 47.4        | 518.2  | 6150.6 |
| Fmsp (harvestable fraction at MSP)   | 0.036  | 0.008  | 0.016       | 0.034  | 0.064  |
| Fraction of harvest reported ( $\gamma = \text{beta}(\alpha, \beta)$ )   | 0.539  | 0.225  | 0.110       | 0.532  | 0.955  |
| $\alpha$ hyperparameter for harvest report rate beta pdf   | 53.52  | 27.40  | 5.77        | 53.97  | 97.87  |
| $\beta$ hyperparameter for harvest report rate beta pdf  | 47.43  | 28.66  | 2.95        | 46.00  | 97.11  |
| Process error variance ( $\sigma^2$ )  | 0.019  | 0.031  | 0.001       | 0.008  | 0.103  |
| Observation error variance ( $\tau^2$ )  | 0.313  | 0.093  | 0.176       | 0.297  | 0.539  |
| (d) Model 4 (production function shape parameter $z > 1$ , harvest report rate $\gamma \sim \text{beta}(\alpha = 3, \beta = 5)$ ); DIC = 378.6 |        |        |             |        |        |
| Carrying capacity ( $K$ , tonnes)  | 1647.0 | 1262.0 | 327.4       | 1283.0 | 5244.0 |
| Intrinsic population growth rate ( $r$ )   | 0.055  | 0.015  | 0.031       | 0.053  | 0.088  |
| Abundance index scaling factor ( $q$ )   | 0.515  | 0.723  | 0.051       | 0.306  | 2.093  |

**Table 2 (Continued)**

| Parameter   | Mean   | S.D.   | Percentiles |        |        |
|---|--------|--------|-------------|--------|--------|
|   |        |        | 2.5%        | Median | 97.5%  |
| Production function shape parameter ( $z$ )       | 2.91   | 1.17   | 1.08        | 2.85   | 4.89   |
| Biomass in 1944 (tonnes)                          | 838.5  | 1254.0 | 135.4       | 426.7  | 4109.0 |
| Biomass in 1973 (tonnes)                          | 429.9  | 491.0  | 50.9        | 273.0  | 1802.0 |
| Biomass in 2004 (tonnes)                          | 1434.0 | 1603.0 | 156.6       | 964.0  | 5499.0 |
| Biomass fraction of $K$ in 1944 ( $P_t = B_t/K$ ) | 0.605  | 0.557  | 0.073       | 0.374  | 1.927  |
| Biomass fraction of $K$ in 1973                   | 0.267  | 0.165  | 0.047       | 0.236  | 0.693  |
| Biomass fraction of $K$ in 2004                   | 0.863  | 0.441  | 0.150       | 0.855  | 1.853  |
| MSP (maximum surplus-production, tonnes)          | 35.49  | 18.33  | 2.61        | 26.40  | 223.44 |
| Bmsp (biomass at MSP, tonnes)                     | 1030.8 | 850.8  | 166.2       | 799.5  | 3649.1 |
| Fmsp (harvestable fraction at MSP)                | 0.034  | 0.008  | 0.016       | 0.033  | 0.061  |
| Fraction of harvest reported ( $\gamma$ )         | 0.358  | 0.158  | 0.095       | 0.346  | 0.693  |
| Process error variance ( $\sigma^2$ )             | 0.018  | 0.029  | 0.001       | 0.007  | 0.097  |
| Observation error variance ( $\tau^2$ )           | 0.312  | 0.093  | 0.177       | 0.298  | 0.541  |

prior (Table 2a–c) are shown in Fig. 2e and compared to the observed nester series from Fig. 1b and the non-parametric smoothing spline nester trend from Fig. 1c. These models fitted the observed and smoothed nester series well with no difference between the posterior median trends from 1973 onwards—nonetheless the annual estimates were again quite imprecise (see Fig. 2f). All models suggest that the Hawaiian green turtle stock was already depleted (perhaps substantially) before the start of the harvest data series in 1944 but that the stock has been recovering since harvesting ceased in 1973. Moreover, it was evident from Model 1 that the stock was seriously over-exploited prior to 1973 (Fig. 3) based on the posterior median trends in the biomass status ( $B/BMSP$ ) and the harvest or fishing mortality status ( $F/FMSP$ ). The posterior median biomass status was  $>1$  from 1999 onwards, which suggest that the stock is well on the way to recovery (Fig. 3a). Based on Model 1, the Hawaiian green turtle stock in 2004 was estimated to have recovered to ca. 83% of pre-exploitation biomass but the precision of this estimate was imprecise (Fig. 2b; Table 2a).

### 3.3. Model sensitivity

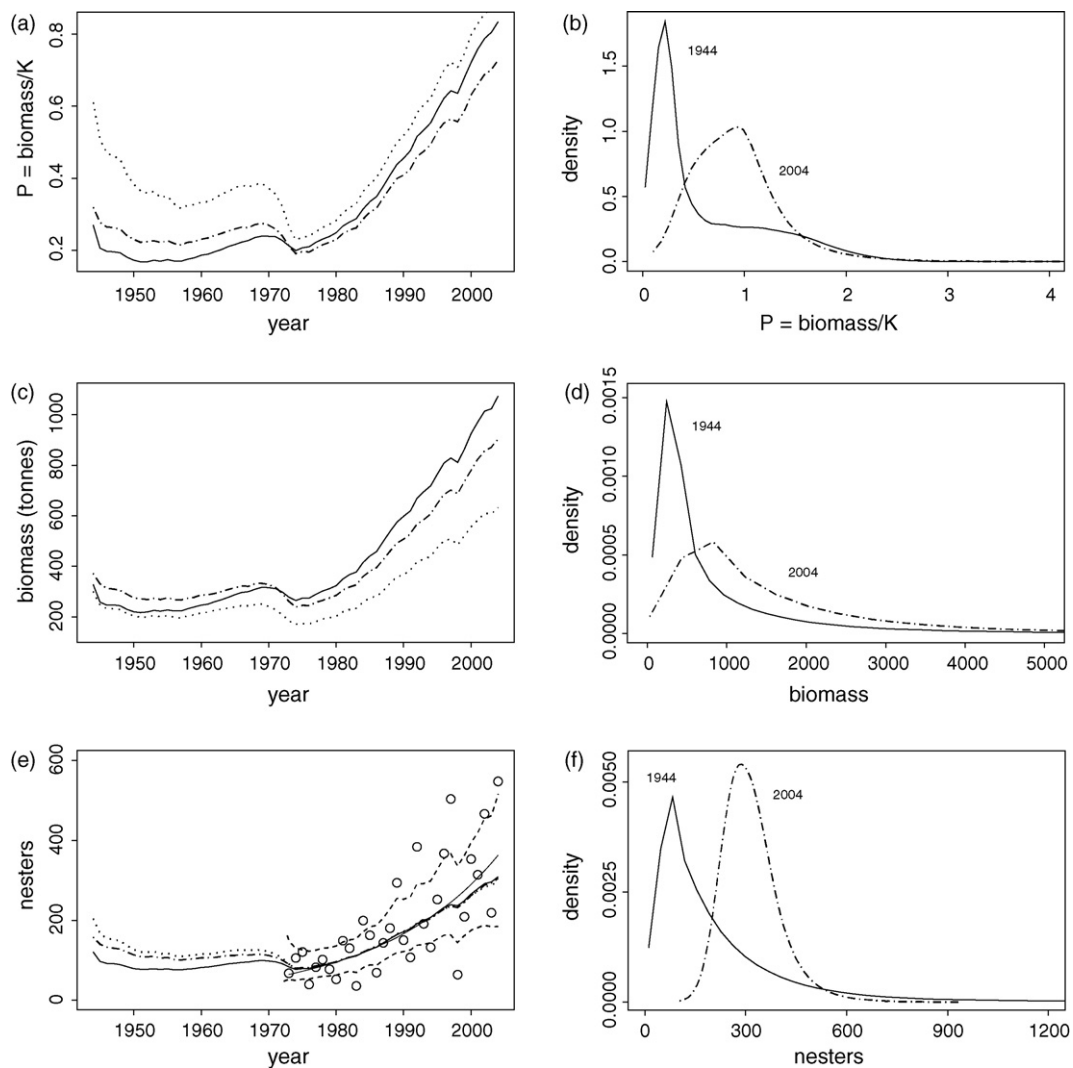
The models summarised in Table 2 used at least one informative prior (Model 4 used three informative priors). These priors were chosen to be vague to reflect a limited knowledge of green turtle demographic processes and parameters (Chaloupka, 2002, 2004). The informative prior used for the intrinsic population growth rate parameter ( $r$ ) had a strong empirical justification (Chaloupka and Limpus, 2001) but this was not the case for the carrying capacity prior ( $K$ ). There was some improvement in precision for  $r$  but little change in the posterior distribution for  $K$  compared to the prior (Fig. 4). The carrying capacity prior was very broad yet the posterior distribution showed no improvement in precision (Fig. 4b), which suggests the data were not strongly informative about carrying capacity. It is important then to evaluate model sensitivity to the carrying capacity prior since  $K$  is one of the most important parameters in surplus-production models (Table 2). However, formal procedures for evaluating Bayesian surplus-production model sensitivity to at least 1 informative prior are not well developed (Millar and Meyer, 2000). One simple but generally useful approach is to specify an alternative form

of the prior such as a vague uniform prior on  $\log K$  instead of the informative lognormal prior for  $K$  (see McAllister and Kirkwood, 1998). This alternative  $K$  prior was implement in Model 3 (Table 2c), which had no effect on estimation of the population growth rate (Table 2, see Fig. 5a). This was not surprising since the  $r$  prior was well defined using a sound empirical foundation. However, a non-informative  $K$  prior did result in (1) a lower carrying capacity  $K$  (Fig. 5b), (2) a lower depletion in 1944 and (3) more significant recovery by 2004 than for instance the model with an informative  $K$  prior. Model 3 also provided more conservative estimates for some management measures such as MSP (Fig. 5c). Moreover, Model 3 provided the least precise estimates of some parameters such as the abundance index scaling factor  $q$  (Table 2). On the other hand, there was no effect of a non-informative prior on management measures such as FMSP or fishing mortality at MSP (Fig. 5d) mainly because FMSP is derived from the better defined population growth rate (Fig. 5a). Accordingly, some parameters such as  $r$  and FMSP are well estimated by all models but parameters such as  $K$  and those defined by  $K$  such as MSP are estimated with substantial uncertainty.

### 3.4. Model application

We illustrate the utility of this Bayesian state-space surplus-production model in the following simple harvest example. The posterior median MSP for Model 1 was ca. 30 tonnes with the posterior median FMSP ca. 0.034 (Table 2a). We evaluated the effect of a constant annual harvest of 30 tonnes on the recovering Hawaiian stock over a 25-year period (2005–2029) using Model 1 with an informative harvest report rate prior  $\gamma$ . The 25-year intervention period reflects around half the generation time of Hawaiian green turtles (Balazs and Chaloupka, 2004b) and so provides sufficient time for the population to respond while 30 tonnes is equivalent to 600 large immature green turtles (see Fig. 6). We compared this 30 tonnes pa harvesting scenario to a scenario that involved a smaller 10 tonnes pa offtake and to a no-harvest scenario. The performance measures were the posterior distributions of predicted relative biomass ( $P_{2029}$ ) and nester abundance ( $I_{2029}$ ) for the three alternative harvest offtakes (0, 10, 30 tonnes) at the end of the 25-year period. Recall also that the stock in

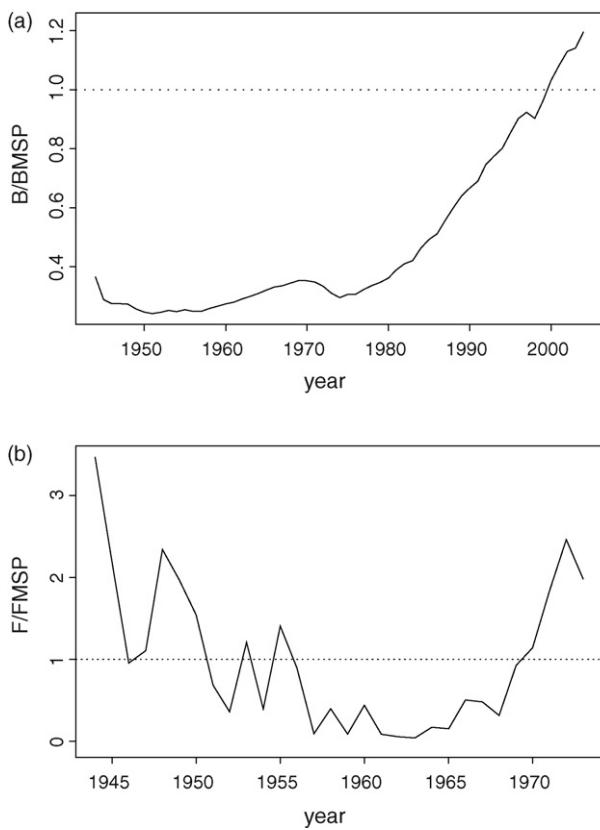




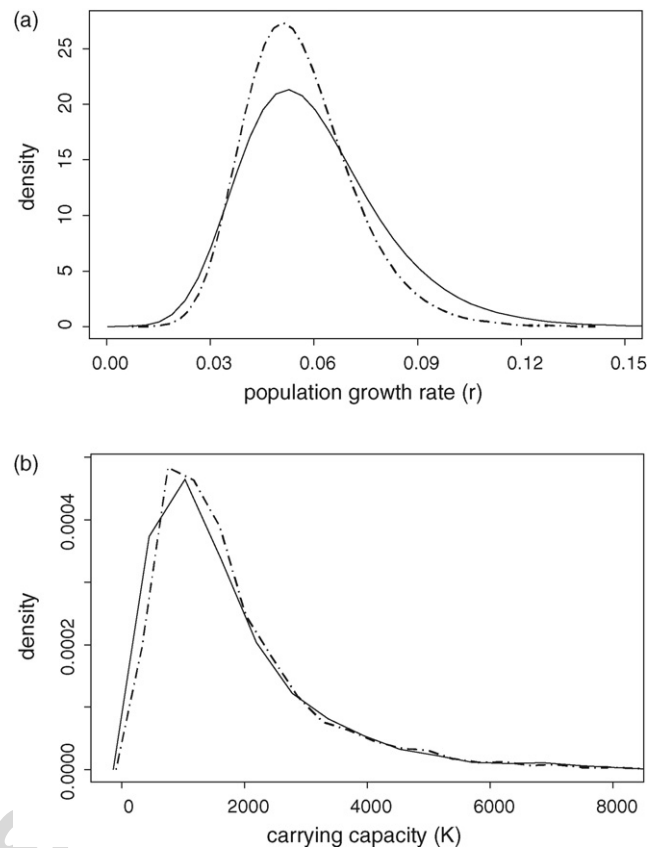
**Fig. 2** – Graphical summary of Bayesian state-space model fits given in Table 2a–c. Panel (a) shows posterior relative biomass medians of the exploitable Hawaiian green turtle stock (1944–2004) for the Pella–Tomlinson surplus-production model with informative lognormal prior on  $K$  (solid curve), logistic function model (dashed curve) and Pella–Tomlinson model with uniform prior on  $\log K$  (dotted curve). Panel (b) show local likelihood density estimates of posterior median distributions of relative biomass at the start (1944) and end (2004) of the data series for the Pella–Tomlinson model with informative lognormal priors on  $r$  and  $K$  (solid curve in Fig. 2a). Panel (c) shows posterior biomass medians of the exploitable Hawaiian green turtle stock (1944–2004) for the same models in (a) while (d) shows the local likelihood density estimates of the posterior median biomass distributions in 1944 and 2004 for the Pella–Tomlinson model with informative lognormal priors on  $r$  and  $K$  (solid curve in Fig. 2c). Panel (e) shows the predicted posterior median nester abundance at the East Island rookery (1944–2004) for the same models in (a) where the open dots show observed nester data, dashed curves show posterior median 95% credible interval for the Pella–Tomlinson model (1973–2004) with informative lognormal priors on  $r$  and  $K$  (solid curve) and thin solid curve shows the smoothing spline fit for comparison. Panel (f) shows local likelihood density estimates of the predicted posterior median nesters distributions in 1944 and 2004 for Pella–Tomlinson model with informative lognormal priors on  $r$  and  $K$  (solid curve in Fig. 2e).

2004 was not fully recovered but estimated ca. 83% of pre-exploitation biomass (Fig. 2a). Therefore, the three scenarios were compared to the posterior distributions of the performance measures in 2004 (see also Fig. 2b and f), which is the end of the data series (Fig. 1) and prior to the start of the simulated harvest period. The posterior distributions of the two predicted population measures ( $P_{2029}$ ,  $I_{2029}$ ) for the three scenarios are shown in Fig. 7. Projecting the stock over a 25-year

horizon leads to uncertain stock abundance estimates but this is an unavoidable consequence of making predictions for a long-lived late-maturing marine species. More extensive data series and perhaps better-constructed priors might improve model fit but not the uncertainty of long-range predictions. The posterior median for relative biomass or nesters is higher in 2029 than 2004 because the stock was very close to  $K$  in 2029 but only  $0.83K$  in 2004 (Table 2a). Harvesting at 10 tonnes



**Fig. 3 – Graphical summary of the Hawaiian green turtle stock exploitation history (1944–2004) shown by posterior median trends in (a) the Bstatus ( $B/BMSP$ ) and (b) the Fstatus ( $F/FMSP$ ) that were derived from the Pella–Tomlinson model with informative lognormal priors on  $r$  and  $K$  (see solid curves in Fig. 2a, c and e). Dotted lines show exploitation benchmarks where Bstatus  $< 1$  and Fstatus  $> 1$  indicate a history of over-exploitation.**

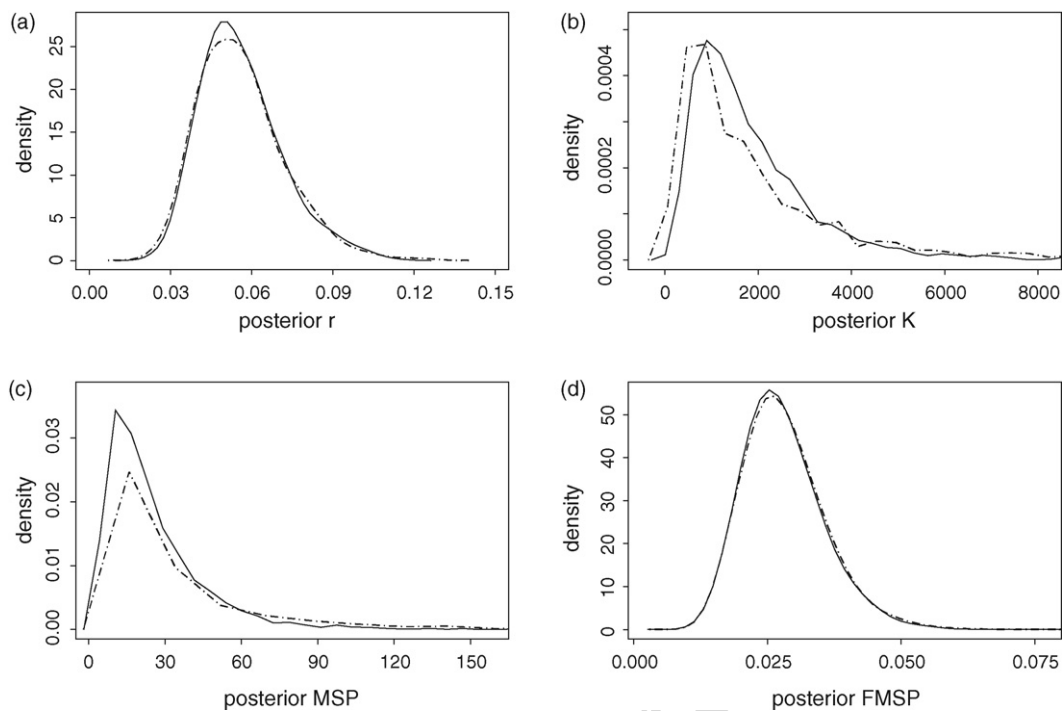


**Fig. 4 – Local likelihood density estimates of the posterior (dashed curve) and prior (solid curve) parameter distributions for Bayesian state-space Pella–Tomlinson model with informative lognormal priors on the model parameters  $r$  and  $K$ .**

pa for 25 years would result in a slightly depleted stock compared to the no-harvest alternative and is similar to either predicted relative biomass (Fig. 7a) or nesters (Fig. 7b) in 2004. Harvesting at MSP (30 tonnes) for 25 years would result in a significantly depleted stock although the predicted depletion level is highly uncertain for relative biomass or nesters (Fig. 7). In fact, maximum surplus-production or MSP occurs at ca.  $0.63K$  (or  $B_{MSP}/K$ ) for the Pella–Tomlinson surplus-production model (Table 2a) and it is this depletion level that is realised in Fig. 7a for the stock harvested at MSP for 25 years. However, it is well known that harvesting at MSP is commercially unsustainable (Hilborn and Walters, 1992) and so some fraction  $p$  of MSP or FMSP such as  $p=0.75$  has been proposed to maximise the yield but minimise the risk to stock viability (Jensen, 2002). Therefore, harvesting the Hawaiian green turtle stock at  $0.75_{MSP} = ca. 23$  tonnes pa ( $0.75_{FMSP} = 0.026$ ) would still reduce the stock but limit the depletion and improve the yield compared to harvesting at the  $MSP = 30$  tonnes ( $FMSP = 0.034$ ). Harvesting the stock at 10 tonnes pa does not deplete the stock anywhere near  $0.63K$ , which results in poor yields but is a far less risky harvest option if long-term viability of the stock is paramount.

### 3.5. Policy simulation tool

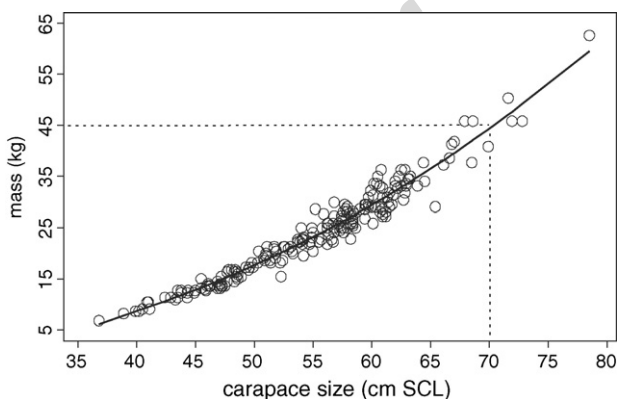
The Bayesian model estimates summarised in Table 2 was used to parameterise the stochastic simulation model equivalent (9). We illustrate the utility of this simulation model using another simple harvest example summarised in Fig. 8, which shows the projected Hawaiian green turtle stock subject to eight constant annual harvest quotas (0, 1, 2.5, 5, 10, 25, 50, 75 tonnes) ongoing for 25 years from 2005. The model included the historical harvest (Fig. 1a) so that the projected stock was recovering from 1973 to 2004 prior to the start of the 25-year simulated harvest period (2005–2029). The stock projections were then continued for a further 20 years to assess subsequent stock recovery after the harvest ceased in 2029. The performance measure was the expected number of green turtle nesters at the East Island rookery. The no-harvest scenario (2005–2029) is shown in Fig. 8a with observed nester abundance superimposed and it shows a similar expected trend to the Bayesian model (cf. Fig. 2e). There was also significant uncertainty in the expected nester abundance from 2005 onwards (cf. Fig. 7b). The remaining panels (Fig. 8b–h) show expected nester trend at the East Island rookery for the seven simulated annual harvest quotas (1, 2.5, 5, 10, 25, 50, 75 tonnes). The quotas  $>25$  tonnes exceed MSP (Table 2d)



**Fig. 5 – Graphical summary of model sensitivity to alternative forms of prior on carrying capacity  $K$ .** Panels show local likelihood density estimates of the posterior distributions for (a) population growth rate  $r$ , (b) carrying capacity  $K$ , (c) MSP and (d) FMSP derived from the Pella–Tomlinson model with informative lognormal priors on  $r$  and  $K$  (solid curve) or uniform prior on  $\log K$  (dashed curve).

and so the expected nester abundance shows the anticipated decline followed by rapid recovery after the simulated harvest ended in 2029 (Fig. 8g and h). Recall that MSP for this Pella–Tomlinson surplus-production model occurs ca.  $0.63K$  so that harvests  $>25$  tonnes will deplete the stock towards  $0.63K$ , which prompts the population to respond with the maximum potential reproductive output presumably due to more food per capita at lower density (Balazs and Chaloupka,

2004b). This density-dependent population response is also evident for a 25 tonnes harvest (Fig. 8f) that is close to MSP for this model (Table 2d). Harvests  $<25$  tonnes (and  $<MSP$ ) show little response as the stock is not significantly depleted at these levels (Fig. 8b–e). Expected nester trends from five scenarios (0, 10, 25, 50, 75 tonnes) are summarised in Fig. 9 so that the expected harvest effects can be readily compared. It is apparent that even a harvest of 10 tonnes pa is expected to slightly deplete the Hawaiian green turtle stock (Fig. 9, see also Fig. 7b). Yet a loss of 10 tonnes pa from all human hazards (fisheries bycatch, directed harvest, boat strike and so on) is unlikely to have a significant impact on long-term stock viability, bearing in mind the significant uncertainty in the estimated trend (Fig. 8e).

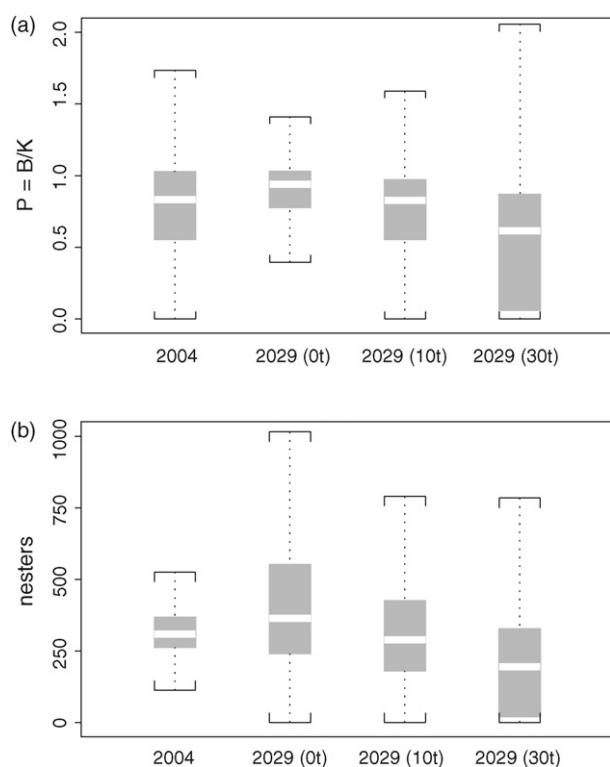


**Fig. 6 – Estimated mass-size function for the Hawaiian green turtle stock drawn from nine different foraging ground population samples.** Solid curve shows a smoothing spline fit to 209 data values (open dots). Dashed lines show that the expected carapace length (cm SCL) of an Hawaiian green turtle at the mean mass of turtles harvested in Hawaiian waters from 1944 to 1973.

## 4. Discussion

### 4.1. Population dynamics model ensemble

We have presented a surplus-production model ensemble that could be useful for developing a better understanding of sea turtle population dynamics when faced with limited data and parameter uncertainty. The ensemble comprised a Bayesian state-space surplus-production model and a complementary stochastic simulation model. Surplus-production or biomass dynamics models are commonly used in fisheries stock assessments when the available data comprise only an aggregate harvest and population abundance time series (Prager, 2002; Punt, 2003).



**Fig. 7** – Boxplot summaries of constant annual biomass loss scenarios (baseline in 2004, 0, 10, 30 tonnes pa) over a 25-year harvest sampling period from 2005 to 2029 on (a) relative biomass ( $B/K$ ) of the exploitable Hawaiian green turtle stock and (b) expected nesting population at the East Island rookery. Projections from Bayesian state-space model (1) with harvest report rate sampled from a  $\text{beta}(3,5)$  pdf. Boxes show interquartile range (25–75th percentile), white horizontal bar in each box = median, bottom and top horizontal capped bars = 10th or 90th percentiles.

This is first application of a Bayesian state-space modelling approach to model sea turtle population dynamics but this approach has been used recently to explore the stock status of tunas (Meyer and Millar, 1999) and large coastal sharks (McAllister et al., 2001). There were no ageclass-specific harvest and demographic information available for the Hawaiian stock so there was little option but to use a Bayesian surplus-production model rather than an age-structured Bayesian state-space model (Rivot et al., 2004). Nonetheless, the simple surplus-production model used here based on a Pella–Tomlinson functional form provided an adequate description of Hawaiian green turtle population dynamics (Fig. 2). Prager (2002) has shown that estimation of the Pella–Tomlinson surplus-production function can be sensitive to data outliers. The Hawaiian green turtle nester abundance series (Fig. 1b) indeed shows significant temporal fluctuations but this is not a consequence of measurement error. In fact, it reflects the nesting variability due to females regularly skipping nesting seasons that is characteristic of most green turtle populations (Chaloupka and Limpus, 2001). Nonetheless, parameter precision might be improved by using a smoothed nester series such as the smoothing spline trend

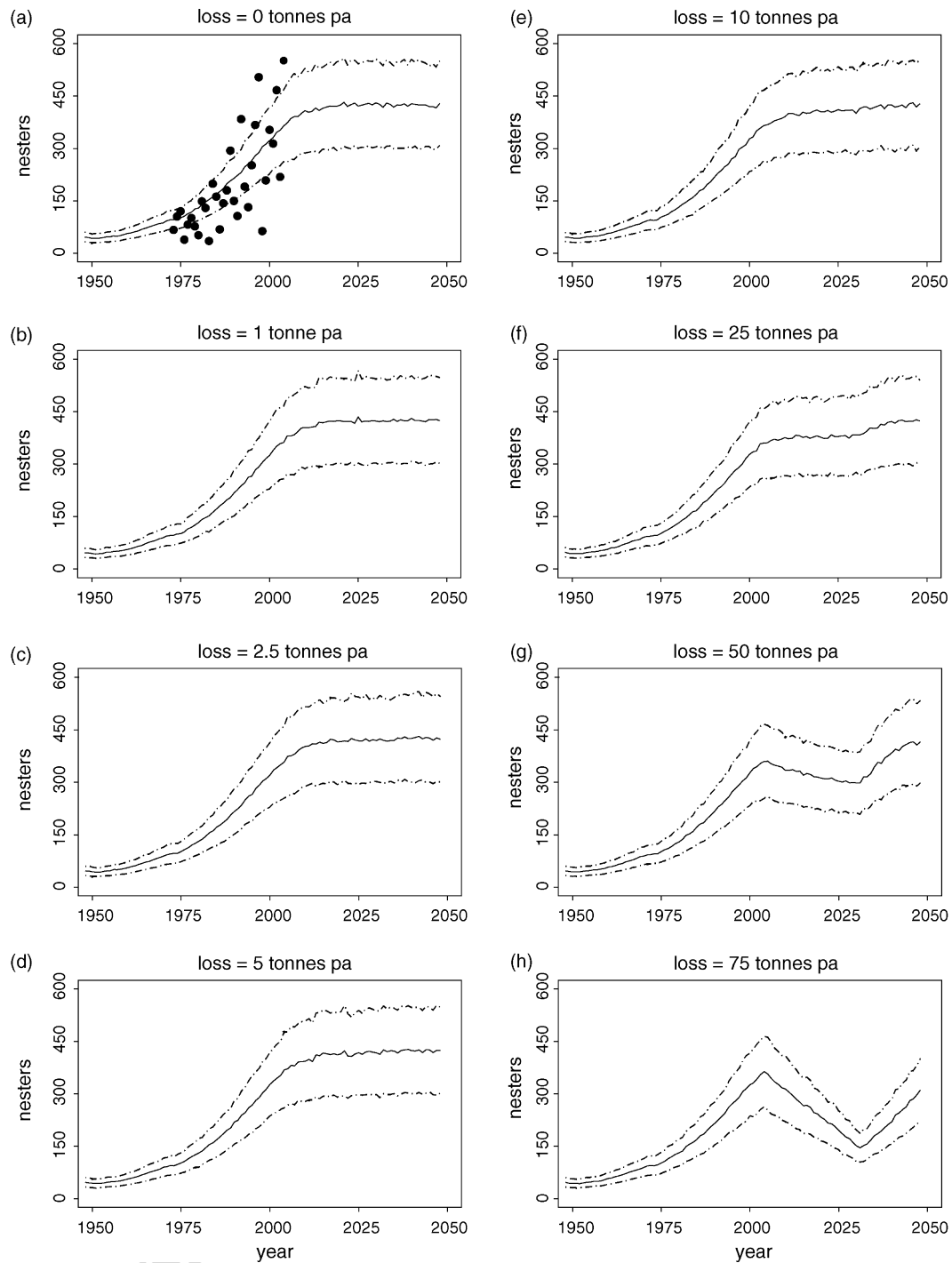
shown in Fig. 2e instead of the observed series to reduce any effect of data volatility on parameter estimation.

Despite data limitations and some imprecise parameter estimates, the Bayesian state-space surplus-production model, nonetheless, provided meaningful estimates of stock status and trend as well as some important population and management measures for the Hawaiian green turtle stock (Table 2; Figs. 2–3). It is anticipated that this model can be used to assess Hawaiian stock recovery status and to determine whether a limited harvest for indigenous cultural purposes might be demographically feasible (Fig. 7), if allowed under the US Endangered Species Act. The Bayesian state-space model parameter estimates were then used to parameterise an easy-to-use stochastic simulation model equivalent that could be more accessible and appealing to interdisciplinary conservation and recovery planning teams. Thousands of Monte Carlo harvest scenario trials for instance (see Fig. 8) can be simulated in a few seconds using the stochastic simulation model equivalent of the Bayesian state-model that can take hours to complete a single scenario run. This model reflects similar behaviour to the Bayesian model, was parameterised using Bayesian model output and is far quicker and easier for policy planning teams to use.

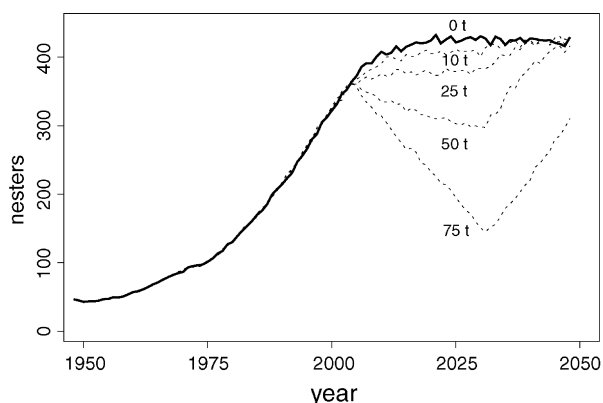
We illustrated the utility of this model ensemble for assessing the recovery and harvest potential of the Hawaiian green turtle stock (see Figs. 7–9). This ensemble of models is also useful for evaluating the impact of incidental capture and drowning of Hawaiian green turtles in local fisheries, which is an emerging management issue in waters around the main Hawaiian islands (Nitta and Henderson, 1993). For instance, it is believed that each year ca. 50 immature turtles are incidentally caught and drowned in Hawaiian inshore and recreational fisheries. A loss of 50 immature green turtles pa is close to the 2.5 tonnes pa harvest scenario shown in Fig. 8c, which suggests that current inshore fisheries bycatch is unlikely to have a significant impact on the long-term viability of the Hawaiian green turtle stock. By no means is this meant to be a comprehensive evaluation of inshore fisheries impacts on Hawaiian green turtle stock viability. But it is illustrative of the complementary application of a Bayesian surplus-production model and a stochastic simulation model equivalent to help evaluate the impact of various human related hazards on green turtle populations given significant data limitations.

#### 4.2. Stock status and trends

Prior to 1974, the Hawaiian stock was subject to significant human exploitation such as turtle harvesting at foraging grounds from the mid-1800s, harvesting of nesters and eggs until the early 1960s, and nesting habitat destruction at the French Frigate Shoals rookery (Balazs, 1980). The Hawaiian stock has increased dramatically since harvesting ceased in 1974 (Fig. 1b) and continues to recover despite some relatively recent but localised outbreaks of a tumour-forming disease, fibropapillomatosis (Chaloupka and Balazs, 2005), and incidental capture in local inshore fisheries (Nitta and Henderson, 1993). So, the once-seriously-depleted Hawaiian green turtle stock is well on the way to recovery and a limited annual harvest <10 tonnes could now be demographically feasible



**Fig. 8 – Summary of constant annual biomass loss scenarios over a 25-year harvest period from 2005 to 2029 on the expected nesting population at the East Island rookery. Projections from stochastic surplus-production simulation model (7) with process and observation error and the harvest report rate sampled from a beta(3,5) pdf based on the median posterior parameter estimates derived from a Bayesian state-space model (Table 2). Panel (a) shows nesting population assuming no additional loss of turtles from anthropogenic sources—dots show the number of nesters recorded from 1973 to 2004, solid curve shows expected curve from 1000 Monte Carlo simulations, dashed curves show  $\pm 1$  standard deviation of the 1000 simulations. Panel (b) shows loss scenario of 1 tonnes pa (20 turtles @ 45 kg each). Panel (c) shows loss scenario of 2.5 tonnes pa (~50 turtles). Panel (d) shows loss scenario of 5 tonnes pa (~100 turtles). Panel (e) shows loss scenario of 10 tonnes pa (~200 turtles). Panel (f) shows loss scenario of 25 tonnes pa (~500 turtles). Panel (g) shows loss scenario of 50 tonnes pa (~1000 turtles). Panel (h) shows loss scenario of 75 tonnes pa (1500 turtles).**



**Fig. 9 – Summary of constant annual biomass loss scenarios over a 25-year harvest sampling period from 2005 to 2029 on the expected nesting population at the East Island rookery. The five curves here reproduce the expected biomass curves from Fig. 8a, e–h on the same scale but without error bands for clarity. Expected curves from Fig. 8b–d not shown as indistinguishable from the 0 tonnes (or no loss) pa scenario.**

(Fig. 8e). These findings concerning the harvest potential are especially relevant for supporting informed public policy debate on the restoration of traditional hunting rights of indigenous peoples in the Hawaiian Archipelago and elsewhere in the Pacific region where traditional practices had previously ensured the sustainable use of marine resources (Kinan and Dalzell, 2005). It is important here to appreciate that a return to commercial harvesting is not being advocated but the point is to simply show that the Hawaiian stock could sustain a small offtake of large-immature turtles for cultural purposes.

#### 4.3. Population and management parameters

The estimated posterior median population growth rate for the best-fit model was well estimated ca. 5.4% pa (3.1–8.9%; Table 2a), which is consistent with estimates for other long-lived late-maturing marine species such as large coastal sharks (Smith et al., 1998), humpback whales (Chaloupka et al., 1999) and manatees (Craig and Reynolds, 2004). Management parameters such as the exploitation rate at MSP (FMSP) were also well estimated because they are based on  $r$  (Fig. 3b). The intrinsic rebound or recovery potential for a stock is equivalent to FMSP (Smith et al., 1998), which was estimated for the best-fit model to be ca. 3.4% (1.6–6.2%). This estimate of FMSP or the recovery potential is also consistent with estimates for other long-lived late-maturing marine species such as large coastal sharks (Smith et al., 1998). Marine species with recovery potentials <4% are generally considered to be highly susceptible to over-exploitation and can take a very long time to recover if seriously depleted (Smith et al., 1998). Early-maturing highly productive marine species such as oceanic sharks and many fishes have high recovery potentials (>8%) and may be comparatively better able to respond to intensive exploitation (Smith et al., 1998). Consequently, the recovery potential (FMSP), or perhaps some fraction of FMSP like

$0.75_{\text{FMSP}}$  (Jensen, 2002), might be a useful biological reference limit for management of a green turtle stock subject to ongoing harvesting. Using management parameters based on the estimated population growth rate ( $r$ ) for a green turtle stock seem to be especially promising because it is one of the parameters that was well estimated using a surplus-production model given limited data availability. While growth rate and associated parameters such as FMSP were well estimated, this was not the case for some other important parameters. For instance, carrying capacity  $K$  was estimated with significant uncertainty, irrespective of the priors used (Table 2). Moreover, the surplus-production model used is sensitive to the choice of carrying capacity prior so that construction of more appropriate  $K$  priors is an important area for future investigation of the Hawaiian stock. Observation error was found to be significantly greater than process error, irrespective of model used (Table 2). This was not surprising because the abundance index used was the observed nester series that displays substantial temporal fluctuations in response to environmental stochasticity (Fig. 1b). Conversely, it is not surprising then that a long-lived, slow-growing and late-maturing species like the green turtle would display little temporal fluctuations in the aggregated stock biomass reflected in the low process error (Table 2). So, it was evident that the limited data available for this study (Fig. 1) were quite informative about parameters or measures like  $r$  and FMSP and the process and observation error but were uninformative about other parameters such as  $K$ .

#### 4.4. Population abundance

It is important to note here that a substantial proportion of a green turtle stock resides in an oceanic developmental habitat (Chaloupka, 2002, 2004) and so is not exposed to harvesting, which occurred exclusively in coastal waters. Moreover, a substantial proportion of the stock resident in coastal habitats following recruitment from an oceanic habitat are too small for any harvesting (Chaloupka, 2002; Balazs and Chaloupka, 2004b). Therefore, only a small proportion of a green turtle stock is exploitable and it is this “exploitable” biomass that is modelled using any form of surplus-production function. The best-fit surplus-production model estimated that the posterior median  $K$  biomass of the exploitable stock was 1431 metric tonnes (Table 2a). The exploitable component of the Hawaiian green turtle stock comprises mainly large immature to mature turtles resident in coastal or neritic habitats, which are turtles >60 cm straight carapace length (>30 kg) and >15 years of age (see Balazs and Chaloupka, 2004b). Turtles <35 cm SCL reside in oceanic habitats and so are not exposed to harvesting while few 35–60 cm SCL coastal habitat turtles would have been harvested historically because of limited size and mass (Fig. 6). The apparent mean turtle mass derived from the reported commercial landings (Fig. 1a) was 45 kg or 70 cm SCL (Fig. 6), so that the exploitable component of the Hawaiian stock at  $K$  would comprise ca. 32,000 45 kg turtles.

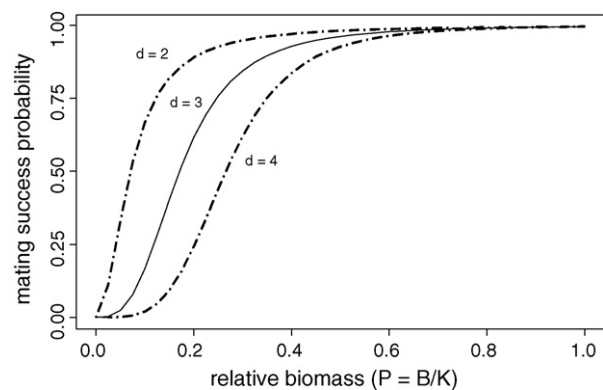
There are no age- or sizeclass-specific composition data available for the Hawaiian stock so it is not possible to directly determine the exploitable fraction of the stock. However, it can be shown that an equivalent exploitable fraction (large immature–mature) of the better-studied southern Great

Barrier Reef green stock would be ca. 10% of that stock (Chaloupka, 2004). Assuming large immature and mature turtles also comprise ca. 10% the Hawaiian stock and that the mean individual mass of these turtles was 45 kg, then it can be estimated that the Hawaiian stock comprises ca. 320,000 turtles at  $K$  (the pre-exploitation abundance). Assuming also that the coastal habitat fraction of the pre-exploitation Hawaiian stock was ca. 23% (Chaloupka, 2004) then it can be estimated that the coastal habitat carrying capacity in the Hawaiian Archipelago is ca. 73,600 green turtles. If the Hawaiian stock is currently around 83% of carrying capacity (Fig. 2a), then there might currently be ca. 61,000 green turtles resident in Hawaiian coastal habitats. There is ca. 2800 km<sup>2</sup> of potential shallow-water coral reef habitat in the Hawaiian Archipelago (Rohmann et al., 2005) and ca. 50% of this estimated area is considered suitable habitat for green turtles in coastal waters (Balazs, unpublished). Therefore, green turtle density in this habitat is 42 km<sup>-2</sup>, which is similar to density estimates for other green turtle populations resident in similar algae-dominated coastal habitats such as the southern Great Barrier Reef (Chaloupka and Limpus, 2001). The estimated coastal habitat abundance is also consistent with the number of females nesting each year at the East Island rookery (Fig. 1b) assuming that mature females comprise ca. 0.6% of a green turtle stock (Chaloupka, 2004), a 1:1 sex ratio (Wibbels et al., 1993) and that ca. 33% of mature females nest each year at the regional rookery (Balazs, 1980; Balazs and Chaloupka, 2004a). So, while all these estimates are uncertain they are highly plausible for population parameters that are extremely difficult to derive for a widely dispersed marine species.

#### 4.5. Density dependence

The Bayesian state-space surplus-production model assumes an “overcrowding” or compensatory density-dependent process affecting the population growth rate at high densities. The 0.63 $K$  maximum productivity estimate for Hawaiian greens (Table 2a) is similar to estimates for other large long-lived marine species such as pinnepeds and cetaceans (Fowler, 1984). These long-lived late-maturing species share the same lack of resilience to exploitation because maximum productivity occurs at higher densities but harvesting can deplete these stocks well below  $K$ . This is one reason why conservative harvest strategies are essential if long-lived marine species such as green turtles are to be exploited on a sustainable basis. So, maintaining the Hawaiian green turtle stock well above 0.63 $K$  would be a prudent conservation objective.

The surplus-production model can be readily extended to include depensatory density dependence or an Allee effect. Depensation involves depressed population growth rates at low densities, which increases the probability of extinction (Dennis, 2002). Depensation could occur for green turtle populations as a consequence of decreased mating encounters at low population density (Chaloupka, 2004), which could then severely restrict the recovery of a depleted population. Reduced mating encounters have been implicated in several population collapses including north Atlantic cod (Rowe et al., 2004) and saiga antelope (Milner-Gulland et al., 2003). Therefore, depensation might be an important process to consider



**Fig. 10 – Morgan-Mercer-Flodin density-dependent mating success function (probability of an Hawaiian female green turtle finding and mating with at least one male given relative density of breeding males and females in the courtship grounds). The curves show the four-parameter function for select values of the shape parameter,  $d$ , where the strength of the Allee effect increases with increasing  $d$ . The curve with  $d = 2$  is similar to the curve estimated by the Bayesian state-space surplus-production model.**

in any assessment of the recovery and harvest potential of the Hawaiian green turtle stock.

Following Dennis (2002), the surplus-production model (4) with a generalised mating encounter probability function is as follows:

$$P_t = P_{t-1} + rP_{t-1}(1 - P_{t-1}^Z) - \frac{H_{t-1}}{K} - f(P_{t-1})P_{t-1} \quad (10)$$

where the probability of not finding a mate  $f(\cdot) = (1 - ((ab + cP_{t-1}^d)/(b + P_{t-1}^d)))$ , which is a Morgan-Mercer-Flodin function (Morgan et al., 1975) with  $a$  = minimum,  $c$  = maximum,  $b$  = rate coefficient,  $d$  = shape parameter. Since  $f(\cdot)$  here is a probability on the  $[0,1]$  interval then  $a=0$  and  $c=1$ . Special cases of the Morgan-Mercer-Flodin function include the hyperbolic or Michaelis-Menten-Monod function ( $a=0$ ,  $d=1$ ; see Fig. 10), which is widely used to model Allee effects (Dennis, 2002), as well as the Hollings and Hill functions used to model nutrient uptake, predator consumption or other density-dependent demographic processes (Morgan et al., 1975). Estimation of the Bayesian state-space surplus-production model (10) provided posterior median estimates of the depensation function parameters  $b=0.002$  (95% credible interval: 0.0003–0.016) and  $d=1.67$  (1.02–4.92). A non-informative inverse-gamma prior was used for  $b$  and a vague uniform prior was used for  $d$ . Based on DIC there was little improvement in model fit compared to any of the models listed in Table 2 but the rate coefficient ( $b$ ) is significantly  $>0$  suggesting the data were informative of an Allee effect. So while the depensation function parameters ( $b$ ,  $d$ ) are quite imprecise for the Hawaiian data, they are nonetheless supportive of some form of hyperbolic-like depensation process (Fig. 10). This is consistent for species with multiple paternity such as the green turtle where a shortage of males (and hence mating encounters) would only be likely at very low population levels. It is apparent for the Hawaiian stock that depensation may occur when the

stock falls well below 5% of the pre-exploitation biomass where the mating encounter probability decreases dramatically (Fig. 10). Hence, compensatory processes could increase the risk of extinction for the Hawaiian stock if it were to be depleted below 5% of pre-exploitation biomass.

It is unlikely that the Hawaiian stock or most other existing green turtle stocks were reduced by human exploitation to such low levels (Chaloupka and Limpus, 2001; Balazs and Chaloupka, 2004a). However, the Cayman Islands green turtle nesting population in the Caribbean was abundant prior to European settlement and was apparently reduced to near-extinction by over-exploitation (Bjorndal et al., 2000). Cayman nesting abundance has shown little recovery over the last century (Aiken et al., 2001) and this may be indicative of depensation compounded by no recolonisation from other regional Caribbean stocks. Depensation was included in recent

stochastic simulation models of the metapopulation dynamics of the southern Great Barrier Reef green turtle stock (Chaloupka, 2004) and it warrants further consideration in the management of green turtle stocks that are subject to harvesting.

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### Appendix A. Bayesian non-linear surplus-production state-space model in WinBUGS with both process and observation error and harvest under-reporting parameter

```
##### using the Millar and Meyer (2000) parameterisation of a Pella-Tomlinson surplus production model #####
model; {##### unobserved state variable P = production = B/K, not assuming B1=K, from 1944-2004 #####
Pinitial ~ dunif(0.01,3)
Pmed[1] <- log(Pinitial)
P[1] ~ dlnorm(Pmed[1],sigma2)
for (t in 2:N) {P[t] ~ dlnorm(Pmed[t],isigma2)
Pmed[t] <-log(max(P[t-1]+r*P[t-1]*(1-pow(P[t-1],shape))-(C[t-1]/RR)/K,0.001))}

##### abundance index based on nesting census at French Frigate Shoals rookery #####
for (t in 1:N) {lmed[t] <- log(q*K*P[t])
l[t] ~ dlnorm(lmed[t],itau2)}

##### noninformative IG prior for process error precision #####
isigma2 ~ dgamma(0.001,0.001); sigma2 <- 1/isigma2

##### noninformative IG prior for observation error precision #####
itau2 ~ dgamma(0.001,0.001); tau2 <- 1/itau2

##### noninformative IG prior abundance index scale parameter #####
iq ~ dgamma(0.001,0.001); q <- 1/iq

##### informative Lognormal prior for carrying capacity K #####
K ~ dlnorm(7.25,1.775) #stdev = 0.75

##### informative Lognormal prior for intrinsic growth rate parameter r #####
r ~ dlnorm(-2.866,9.615) #stdev = 0.32

##### vaguely informative prior for shape parameter of the Pella-Tomlinson surplus production model #####
shape ~ dunif(1,5)

##### noninformative beta prior for harvest report rate RR #####
RR ~ dbeta(alpha,beta) #catch report rate from beta pdf with hyperparameters alpha and beta
alpha ~ dunif(1,100) #hyperparameter with hyperprior from a uniform pdf
beta ~ dunif(1,100) #same for alpha

##### stock abundance estimates #####
for (t in 1:N) {B[t] <- P[t]*K} #estimated biomass (tonnes) from 1944 to 2004
for (t in 1:N) {nesters[t] <- (q*K*P[t])} #estimated FFS nesters from 1944 to 2004

##### harvest management parameters #####
MSP <- FMSP*BMSP; FMSP <- r/(pow((shape+1),(1/shape))); BMSY <- K/(pow((shape+1),(1/shape)));
for (t in 1:N) {F[t] <- (C[t]/RR)/B[t]; Fstatus[t] <- F[t]/FMSP; Bstatus[t] <- B[t]/BMSP}

##### input data files and initial conditions #####
```



## Appendix B. Non-linear stochastic simulation model in MADONNA with process and observation error and parameters based on Bayesian non-linear state-space model

METHOD RK4 #4<sup>th</sup> order Runge-Kutta integration method; STARTTIME = 1944; STOPTIME = 2044; DT = 1

```
{Pella-Tomlinson form of surplus production}
d/dt(biomass) = (rmax*biomass_delay*(1-(biomass_delay/K)**shape)-harvest_delay)
INIT biomass = 329 {tonnes}; shape = 2.94; rmax = 0.0544; K = 1431
delay_time = 1; biomass_delay = if time = 1944 then biomass else delay(biomass,delay_time)
P_Inorm = biomass_Inorm/K {biomass as a function of K and process error}

{harvest data in tonnes with constant loss scenarios starting in 2005 for 25 year duration}
harvest_delay = if time < 1974 then delay(harvest,delay_time)/report_rate else quota1
quota1 = if time > 2004 and time < 2031 then quota else 0: quota = 0

{harvest report rate}
RR_switch = 1; report_rate = if RR_switch=1 then report_rate1 else report_rate2
report_rate1 = 0.346 {estimated from WinBUGS model or use the beta pdf below}
report_rate2 = (alpha/(alpha+beta))*scale {see beta pdf below}

{beta(3,5) pdf for report_rate derived using convolution of gamma functions}
alpha = gamma1_pdf; beta = gamma2_pdf; scale = 1
gamma1_pdf = arraysum(r[*]) {gamma(1,3) pdf with location = 0}
r[1..v] = -logn(random(0,1)); v=3 {=alpha from WinBUGS model}
gamma2_pdf = arraysum(s[*]) {gamma(1,5) pdf with location = 0}
s[1..w] = -logn(random(0,1)); w=5 {=beta from WinBUGS model}

harvest = GRAPH(time) {reported landings in tonnes}
{read data file here}

{lognormal process error}
biomass_Inorm = exp(normal(biomass_lognorm_mean,biomass_lognorm_sd)+biomass_lognorm_var/2)
biomass_lognorm_mean = logn(biomass)-0.5*biomass_lognorm_var
biomass_lognorm_var = logn((((biomass*biomass_cv)^2)/(biomass^2))+1)
biomass_lognorm_sd = sqrt(biomass_lognorm_var)
biomass_cv=0.1

{lognormal observation error}
nesters_Inorm = exp(normal(nesters_lognorm_mean,nesters_lognorm_sd)+nesters_lognorm_var/2)
nesters_lognorm_mean = logn(nesters)-0.5*nesters_lognorm_var
nesters_lognorm_var = logn((((nesters*nesters_cv)^2)/(nesters^2))+1)
nesters_lognorm_sd = sqrt(nesters_lognorm_var)
nesters_cv=0.29

{stock abundance measures}
P = biomass/K; nesters = (q*biomass); q = 0.287 #scale parameter

{harvest management parameters}
MSY = FMSY*BMSY; FMSY = rmax/((shape+1)^(1/shape)); BMSY = K/((shape+1)^(1/shape));
depletion = biomass_Inorm/BMSY; Bstatus=biomass/BMSY
```

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