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The operating model

The model developed for the present study is a stage/size-structured metapopulation model of the school prawn stocks inhabiting the Clarence River. It includes individual-based population dynamics and movement between compartments that are both subject to the effects of temperature and river discharge. Three fisheries exploit the modelled population with the fisher dynamics based on a combination of historical effort levels and changes in catch per unit of effort. The model is calibrated to 20 years of past catch data from the Clarence River fisheries using a Bayesian SIR approach which produces a 'posterior' distribution from likely parameter values and the model runs which best fit the data.

Individual growth

A suitable individual growth function for penaeid shrimp is the von Bertalanffy growth function (Garcia and Le Reste 1981):

$$l = L_\infty(1 - \exp(-k(t - t_0))) \quad (1)$$

where l is the carapace length of the prawn at time t, L_∞ is the average asymptotic carapace length to which an individual grows (mm), k is a species-specific growth-rate constant (per months), and t_0 is the theoretical age (in months) of the individual at zero carapace length.

Rather than implementing a fully length-structured or agent-based model, we chose to aggregate prawns into groups based on growth functions (Walters and Martell 2004, box 5.3). Variability in growth within a cohort was accomplished by dividing each cohort into 10 aggregates (five for each sex), with each aggregate associated with a separate growth function (Punt et al. 2001). Newly spawned individuals of each sex were added to one of the five growth aggregates according to the proportions of $5\% : 25\% : 40\% : 25\% : 5\%$. Thus,

the majority of prawns were placed in the central growth aggregate, which represents the best-estimate for prawn growth. The remaining prawns were placed in aggregates with growth rates above and below this best-estimate rate, giving the overall distribution of growth a normal-like variability around this central growth rate.

The median (best-estimate rate) von Bertalanffy growth parameters were based on the estimations for growth made in the Clarence River by Glaister (1977, p. 41) and weight for both sexes was calculated using the length-weight provided by Broadhurst et al. (2004) from studies conducted in the Clarence River (see Table 1 for details). Both male and female prawns were explicitly included in the model; however, to simplify the notation, only a single sex is represented in the following equations. Each of the following equations should be assumed to apply to both sexes unless otherwise specified.

Prawns of different sizes were divided into seven 5-mm categories, each of which belonged to one of three different life stages, namely larvae (<5 mm CL), juveniles (5 mm and <20 mm CL) and adults (20 mm CL) (see Fig. 2 in main publication). In this model, a larvae was classified as a prawn that is less than 5 mm CL, although juveniles as small as 3 mm can recruit to the estuary fisheries (Glaister 1977). The size stages were used to reduce the number of parameters in the model, while still allowing for size-dependency in key processes (such as mortality) (Werner and Gilliam 1984).

Mortality

Total mortality (Z) was modelled separately for the three life stages. Although no studies were found that provided estimates of larval natural mortality, the rate is believed to be high on the basis of the fecundity of this species (Dall et al. 1990). Values for the juvenile mortality rate were also unknown, and thus these two parameters became the primary means by which the model was calibrated to the combination of historical catch records and average prawn weight data. A sensitivity analysis was also completed (section 2.10.2) to examine the effect of changes in these parameters.

Thus, numbers of prawns of carapace length class l in zone A in month t+1 ( ) were calculated as shown in Equations 2 and 3, where t represents time, $N_{l,t}^{A}$ represents numbers of prawns of carapace length class l in zone A in month t. Element $\ddagger_{k \to l,t}^{A}$ is the fraction of prawns in length class k in zone A that move to length class l during the time step t for all five growth aggregates. This element was calculated by determining the fraction of prawns in length class k that move to class l, and then weighting this co-efficient in proportion to the distribution of growth aggregates. M_l is the natural mortality of prawns of carapace length class l, $Z_{l,t-1}^{A}$ is the total mortality for prawns of carapace length class l in zone A during the previous month (t-1), $F_{l,t}^{A,X}$ is fishing mortality induced on prawns of carapace length class l by fleet X in zone A during month t, and S_{l}^{X} is the retention selectivity of the gear used by fleet X on the stock of carapace length l.

$$N_{l,t}^{A} = \sum_{k=1}^{L} \ddagger_{k \to l,t}^{A} \cdot N_{k,t-1}^{A} e^{-Z_{k,t-1}^{A}}$$

(2)

$$Z_{l,t}^{A} = M_l + \sum_{X} S_{l}^{X} F_{l,t}^{A,X}$$

(3)

Individuals were harvested from the model's two fishing zones, based on the Baranov catch equation. The catch of prawns of carapace length l in zone A in month t was calculated as:

$$C_{l,t}^{A} = \frac{\sum_{X} S_{l}^{X} F_{t}^{A,X}}{Z_{l,t}^{A}} \cdot N_{l,t}^{A} \cdot (1 - \exp(-Z_{l,t}^{A}))$$

(4)

The total catch for a zone was calculated by summing the mean weights of all the length classes.

Selectivity (S_{l}^{X}) was calculated using a logistic selection curve (Wileman et al. 1996, p. 40) as:

$$S_{l}^{X} = \left(\frac{\exp(a + bl)}{1 + \exp(a + bl)} \right)$$

(5)

where a and b are calculated on the basis of the length of species at 50% retention (L_{50}^{X}) and the selection range of the gear (SR^{X}) for fleet X:

$$L_{50}^{X} = \frac{-a}{b}$$

(6)

$$SR^{X} = L_{75} - L_{25} = \frac{2.197}{b}$$

(7)

The fishing mortality ($F_{l}^{A,X}$) resulting from fleet X in zone A, during time t, was calculated using the observed effort applied by the fleet in that zone, the catchability of the prawns or the efficiency of fleet X (q^{X}):

$$F_{t}^{A,X} = (1 + u)^{t} q^{X} \cdot E_{t}^{A,X}$$

(8)

where $E_{t}^{A,X}$ is the effort (boat-days) of fleet X in zone A during time t, and   is the monthly growth in fleet efficiency (technology creep), which for simplicity is regarded as the same for each of the fleets .

Effort data from the three fisheries from 1986 to 2005 were available from NSW DPI, but a model of effort dynamics was required to represent catches from 2006 and beyond. For each of the three fisheries, future effort (2006 onwards) was a combination of the historical fraction of the annual prawn catch harvested that month ($\cdots^{m}$), multiplied by a factor that reflected the catch rate (CPUE) at the beginning of each month (see section 2.8 for more details on the chronology of processes). This representation modelled the behaviour of fishers who intensified their effort if fishing early in the month was successful, and reduced their effort if fishing was poor.

$$E_{t(y,m)}^{A,X} = (\ldots_m \sum_{y=1986}^{2005} E_{t(y,m)}^{A,X}) . \exp\left(\frac{(U_t - U_b)}{\mathsf{X}}\right) \quad (9)$$

In Equation 9,   is the effort (boat-days) of fleet X in zone A during month m of year y, Ut is the sampled CPUE at time t, Ub is a constant base CPUE value around which changes to effort are generated, and   is the parameter used to connect changes in CPUE to changes in effort. Note that future fishing effort was subsequently modified by closures for each fleet if prescribed in the management strategy (i.e. effort was set to zero).

Fecundity and recruitment

In penaeid populations, individuals are generally short-lived (i.e. <3 years) but females may spawn a number of times in a year (Bagenal 1973; Penn 1980). The most important factors in determining prawn fecundity include water temperature, size of individual females and moult frequency during spawning season. All of these factors affect the number of eggs produced and the number of times a female will spawn each year (Penn 1980). In this model, we simplified these processes and assumed that fecundity is a function of the carapace length of females. Females above an average carapace length of 25 mm were treated in the model as sexually mature (range 18–30 mm CL) (Glaister 1978b, p. 552) and after sexual maturity is reached, any further increases in carapace length translated into increased fecundity ((Penn 1980) with western school prawn Penaeus latisulcatus).

Recent studies have provided good evidence for the existence of a stock–recruitment relationship in penaeid prawns (Ye 2000). In this model, egg production was linked to larval population numbers using a Beverton–Holt stock–recruitment function (reparameterised as in Haddon (2001) to the steepness of the stock–recruitment relationship and the initial biomass/recruitment). The stock–recruitment relationship employed is as follows:

$$R_t = \frac{(\Gamma_t)}{A^{sr} + B^{sr}(\Gamma_t)} . \exp(e_t) \quad (10)$$

$$\Gamma_t = \sum_l N_{l,t}^{female} f_l \quad (11)$$

$$A^{sr} = w_L\left(1 - \frac{z - 0.2}{0.8z}\right) \quad (12)$$

$$B^{sr} = \frac{z - 0.2}{0.8 \cdot z \cdot R_v} \quad (13)$$

where R_t is the number of recruits (prawn larva) produced in month t, $\_t$ represents the number of eggs produced by the spawning stock at time t, A^{sr} and B^{sr} are the parameters of the Beverton–Holt stock–

recruitment relationship, e is the normally distributed recruitment error,   is the number of female prawns of carapace length l in month t,   represents the fecundity of female prawns of carapace length l, wL is the average weight of a prawn larva recruit (calculated using the length to weight relationship given in Table 1), z represents the steepness of the stock–recruitment relationship and Rv is the initial recruitment used for the simulation. In this context, a recruit was defined as a prawn larva (<5 mm CL). Because spawning females may produce eggs in any zone, the number of recruits produced in each zone was made proportional to the number of eggs produced in each zone.

Movement (immigration and emigration)

The typical life-cycle of the eastern school prawn begins when adults spawn in ocean waters. The larvae immigrate on lunar tides (Rothlisberg and Church 1993) into estuaries and up-stream towards suitable habitats, such as seagrass beds, where they settle. The post-larvae that survive the high larval mortality grow into juvenile prawns in the non-fishing zones. The juveniles then move downstream into the estuary fishing zone, possibly before any appreciable growth occurs (Coles and Greenwood 1983). Once in the estuary zone the prawns grow until they approach sexually maturity, at which time they begin to move to the ocean zone to spawn.

Movement between compartments was calculated each month according to coefficients as shown in Equation 14.

$$N_{l,t+1}^{A_1} = N_{l,t}^{A_1} - \eta_{ls,t}^{A_1 \rightarrow A_2} N_{l,t}^{A_1} + \eta_{ls,t}^{A_2 \rightarrow A_1} N_{l,t}^{A_2} \quad (14)$$

where $N_{l,t}^{A}$ is the number of prawns of carapace length-stage l in zone A and $\eta_{ls,t}^{A_2 \rightarrow A_1}$ is the proportion of individuals of length-stage ls (larva, juvenile or adult) moving from zone A_2 to A_1 at time t. Each length-stage can move between any connected compartments, however the movement of juveniles and adults is primarily in the seaward direction, while larvae move into the estuaries from the ocean. The values of the $\eta_{ls,t}^{A_2 \rightarrow A_1}$ parameters had a base value in the model but they do not stay constant as they are manipulated by environmental factors (described in the following section).

Climate variability and its influence on population dynamics

The calibration of the EPT and OPT catches to the model presented a challenge that provided some interesting insights into the dynamics of this system. Although there appeared to be sufficient evidence to assume that river discharge events affected the seaward migration of prawns, there were two alternative hypotheses we could have considered that would have allowed us to match both the relatively stable EPT catches and the more variable OPT catches that spiked during high river discharge events. We could have assumed that a population of adults inhabited the unfished zone and migrated rapidly out to the ocean during rain events; or alternatively, we could have taken the approach that high river discharge events resulted in increased growth of prawns and/or increased catchability. The later approach was chosen primarily on the basis of the evidence

presented in the movement and distribution studies on this species, which showed a consistent trend of increasing prawn size with closer proximity to the ocean during normal climate conditions (graphically presented at the bottom of Fig. 2 in main publication) (Glaister 1978b; Coles and Greenwood 1983). The specifics of how we modelled such river discharge effects are as follows.

The impact of river discharge on the growth and movement of school prawns

The exact mechanism by which high river discharge affects the school prawn's seaward emigration has been debated since the 1950s. An examination of school prawn populations in several NSW estuaries concludes that the emigration of prawns after flood events is due to the resultant decreased salinity (Racek 1959). However, a separate study of school prawns in the Hunter River, NSW, shows that a heavy flood event can have a more pronounced effect on emigration than a more moderate flood, even though the latter flooding is sufficient to reduce the estuary salinity levels to that of freshwater (Ruello 1973b). Ruello's research suggests that the enhanced emigration is instead due to increased river flow and subsequent disturbances of bottom sediments. Studies on the effect of rainfall on the emigration of banana prawns in the Gulf of Carpentaria relate migration to the tolerance of juvenile banana prawns to low salinities but also suggest that rainfall may affect banana prawn productivity also through increases in nutrient levels in the water, which then increase growth and survival (Vance et al. 2003). Several further mechanisms have been proposed for the link between freshwater flow and different fishery species, including: (i) trophic linkages via changes to primary or secondary production due to increased nutrient levels in water; (ii) changes in distribution due to altered habitats; and (iii) changes in population dynamics including recruitment, growth, survival and abundance (Robins et al. 2005).

For the purposes of this model, we used salinity as a proxy for all possible causes for prawn emigration after flood events. Salinity was set at base levels and then allowed to decrease as river discharge events occurred. Each compartment had a recovery rate which allowed the salinity levels to return to their base levels over time. By employing this process we hoped to incorporate a lag effect of a large river discharge event which would enable the prawns to emigrate seaward even after the discharge event diminished.

The effect of river discharge and temperature on prawn movements is through alteration of the movement parameter values $m_{ls,t}^{A_2 \rightarrow A_1}$ (Equation 14). Each movement parameter was adjusted by river discharge and temperature, as shown below in Equation 15.

$$If \ sa_t^A \geq sa_b^A \quad m_{ls,t}^{'A_i \rightarrow A_j} = m_{ls,t-1}^{A_i \rightarrow A_j}$$

$$If \ sa_t^A < sa_b^A \quad m_{ls,t}^{'A_i \rightarrow A_j} = m_{ls,t-1}^{A_i \rightarrow A_j} \zeta^A \exp(sa_b^A - sa_t^A) \quad (15)$$

where ζ^A is the salinity movement effect factor for area A, sa_t^A is the salinity level in area A at time t and sa_b^A is the base salinity level below which an effect occurs.

High river discharge events are believed to also affect the growth of juveniles (Ruello 1973b) by increasing the availability of water borne food for the prawns who are detritus feeding opportunistic omnivores (Kailola et al. 1993). Fishers refer to this food-enriched water as 'sweet water'. This phenomenon is believed to result from the disturbance of benthic communities during flood events (Jones 1987) and from the increased primary and secondary production generated by increased nutrient levels (Moore et al. 2006). To incorporate this hypothesised impact on growth, a food availability level was added to each compartment in the model. High river discharge temporarily increased the food availability level in each compartment at the same time that it reduced salinity. Just as there was a recovery rate for salinity there was also a loss rate associated with food availability.

Food availability affects growth through the manipulation of the k values in Equation 1, as shown below in Equation 16,

$$k' = k \cdot g^A \exp(fa_{t-1}^A - fa_b^A)$$ (16)

where ^{A} is the food availability growth effect factor for area A that is used to calibrate the effect on growth, fa_{t-1}^A is the food availability level in area A at time $t-1$ and fa_{t-1}^A is the base salinity level above which an effect occurs.

The impact of temperature on the growth and movement of school prawns
The advent of spring, and associated increases in water temperature, coincides with a rapid growth of M. macleayi and an immigration of maturing prawns to ocean waters (Glaister 1978a). The link between growth rates and water temperatures has been well confirmed by research of penaeid prawns (Racek 1959; Ruello 1973a; Glaister 1977, p. 40; Potter et al. 1986, Potter et al. 1989; Somers 1990) as well as of other crustacean species (Koeller 1999; Drinkwater et al. 2006) and of marine life in general (Neuheimer and Taggart 2007). To incorporate this effect, the k values in the von Bertalanffy growth function (Equation 1) were manipulated such that the minimum growth rate occurred when water temperatures were at their lowest levels and the maximum growth occurred when water temperatures were at their highest levels (Lhomme, 1977 as cited in Garcia and Le Reste 1981). Although there is evidence to suggest that water temperature also has an effect on prawn survival (Vance et al. 2003), to simplify this model we restricted the effect of water temperature to its effect on growth.

Temperature was also used in the model as an indicator of the seasons that drive seaward emigration. Research has found a continuous recruitment of pre-juvenile M. macleayi to the Clarence River estuary (Glaister 1977, p. 39), with the main peak of this recruitment occurring in the summer and early autumn months (Racek 1959; Ruello 1973a; Coles and Greenwood 1983, p. 740). Larval upstream movement occurs throughout the year but peaks at times when spawning peaks in ocean waters (Glaister 1977; Rothlisberg and Church 1993). To incorporate such seasonality into the model, a seasonal element based on temperature was added so that there was a peak in seaward movement of juveniles during summer months.

The effect of river discharge (D_t) and temperature (Tt) on growth is through manipulation of the k values in Equation 1 as shown below in Equation 17:

$$k' = k(1 + Œ_1 \cdot D_t + Œ_2 \cdot T_t) \quad (17)$$

where $_1$ and $_2$ are the coefficients of the effect on growth of discharge and temperature respectively.

The effect of river discharge and temperature on prawn movements is through alteration of the movement parameter values (Equation 14). Each movement parameter was adjusted by river discharge and temperature as shown below in Equation 18.

$$\mu'^{A_i \rightarrow A_j}_{ls,t} = \mu^{A_i \rightarrow A_j}_{ls,t}(1 + \{_1 \cdot D_t + \{_2 \cdot T_t) \quad (18)$$

where $_1$ and $_2$ are the coefficients of the effect on prawn movements of river discharge and temperature respectively.

Other impacts of river discharge on school prawn dynamics

Large river discharge events have been speculated to also affect the fecundity of school prawns and hence the number of recruits in subsequent years. The high densities of prawn numbers following rain events are believed to help improve a prawn's chances of mating and spawning (Ruello 1973b). Another possible result of river discharge events is an increase in schooling behaviour which can increase catchability (as has been found to be the case with other penaeids (Penn 1984; Vance et al. 2003, p. 48; Zhou et al. 2007; Prince et al. 2008)).

The reasonably good calibration achieved for this model was attained without river discharge directly affecting fecundity; however, the effect of river discharge on growth indirectly increases the fecundity of the population as fecundity is linked to size (section 2.5). We have also permitted catchability to be affected by river discharge according to Equation 19:

$$If \; D_t > D_E \quad q^{X*} = q^X \cdot y \cdot D_t \quad (19)$$

where is the coefficient of the effect of river discharge on catchability that occurs when discharge level Dt exceeded the amount chosen as the 'river discharge event' level DE (see Table 1 for more information). This effect was limited to the month of high river discharge events, and at most, the catchability doubled during these.

Chronology of processes

The smaller the time-step in a simulation model, the less the chronology of processes affects outcomes. In the present study, we were restricted to monthly steps which were the temporal resolution of the catch and effort data. The ordering of processes was based on the chronology used in ISIS–Fish model (Mahevas and Pelletier 2004) and modified to suit the model presented here (Fig. 1).
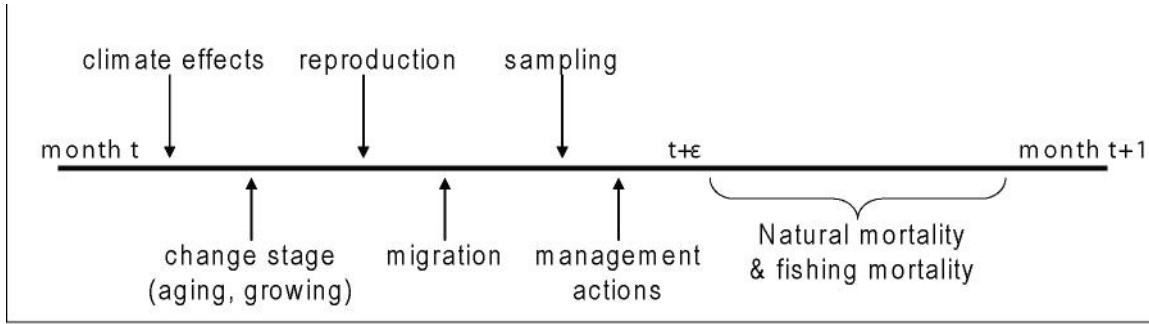
Fig. 1. Diagram showing the order of processes used in the simulation model.

Model calibration

Step 1: Manual calibration

The first step in the calibration of the model involved matching the output from the model with 21 years of existing catch history for the ocean and estuary fisheries that operated in an around the Clarence River. Where reliable values were not available for parameters they were manually adjusted so that the observed and expected catches became aligned (see Table 1 for a list of the parameter values used and their sources). A cost function was applied to determine the quality of the fit of the modelled to the observed catch records from 1985 to 2005 for each of the three fisheries. Evaluating the calibration of the model to the catch records of the three separate fisheries in the two separate fishing zones provided a structural validation of the model (Aumann 2007) by showing that the model mimics the source system on a step-by-step and component-by-component basis. The cost function used was (Moll 2000):

$$\Delta^X = \sum_{t=1985-01}^{2005-12} \frac{\left| (C_t^X - O_t^X)/\dagger^X \right|}{n^X} \tag{20}$$

where Δ^X is the cost function for fleet *X*, time *t* is measured in months from Jan 1985 to Dec 2005, C_t^X is the modelled prawn catch for fleet *X* in time *t* (kg), O_t^X is the observed prawn catch for fleet *X* at time *t* (kg), $\dagger^X$ is the standard deviation of the observed data for fleet *X*, and n^X is the number of catch record data points for fleet *X*. The fit for each fleet was classified according to the (subjective) interpretation supplied by OSPAR Commission (cited in Moll 2000) which is: very good: <1 standard deviation, good: 1 or 2 standard deviations, reasonable: 2–5 standard deviations, poor: >5 standard deviations.

Step 2: Sensitivity analysis

A sensitivity analysis was conducted against each of the model parameters in order to determine the key drivers of the model (Arhonditsis and Brett 2004). Each parameter value (input) was increased and decreased 20% and the effect on a number of model outputs (management indicators) was recorded. This process was repeated 20 times with different random numbers used each time (i.e. a total of 60 records for each

parameter). The results were then used as the dataset for a step-wise regression analysis with the purpose of developing best-fit equations (Kleijnen 1995). The resulting regression equations provided approximations of the input/output behaviour of the simulation model. A single multiple-linear regression equation was used which implicitly assumed that interactions between input parameters were insignificant (Equation 21).

$$Y_i = \mathsf{S}_0 + \sum_{h=1}^{H} \mathsf{S}_h x_{ih} + \mathsf{V}_i \qquad (21)$$

$$(i = 1,...,n)$$

where Y_i is the simulation response (management indicator) to a model run i (involving a certain combination of initial parameter values), $_0$ is the regression intercept, $_h$ is the first order effect of parameter h, x_{ih} is the value of the standardised parameter h in combination i, $_i$ is the error term of the regression model for parameter combination i, and n is the number of simulated parameter combinations.

In this equation, each parameter h must be standardised for the first-order effects $_h$ to reflect the *relative* importance of each parameter. So z_h as the original (non-standardised) value of parameter h, which ranges between minimum value and maximum value, the spread of parameter h can be measured by $a_h = (\max(h) - \min(h))/2$ and the mean of parameter h can be measured by $b_h = (\max(h) + \min(h))/2$. The standardised value x_h can then be calculated as (Kleijnen 1995):

$$x_{ih} = (z_{ih} - b_h)/a_h \qquad (22)$$

Three management indicators where chosen as model outputs (Y_i), namely the Future Average Annual Ocean Prawn Trawl catch from Jan 2006 to Dec 2015; the Future Average Annual Estuary Prawn Trawl catch from Jan 2006 to Dec 2015; and the Future Depletion Ratio of prawn stock, which is the ratio of estimated Biomass in 2015 to Estimated Biomass in 1985. A regression analysis was performed against each of these management indicators to determine the key parameters (drivers) for each of them as dictated by the mechanics of the simulation model.

Step 3: Bayesian SIR calibration

The Bayesian approach used in the present study estimated the posterior probability distributions of key parameters by the sampling/importance resampling method. Five parameters were chosen as 'key parameters' and given a prior probability distribution function (pdf). The choice of these five parameters was based on their importance in the model as shown by the sensitivity analysis and by the level of uncertainty associated with their values.

Monte Carlo methods such as Markov Chain Monte Carlo and importance sampling are the most frequently used methods for Bayesian analysis. For the purposes of the present study, we chose to use the sampling/importance resampling (SIR) method which was numerically robust and straightforward to

implement (McAllister et al. 1994). The SIR algorithm involves two distinct phases. Phase one draws a value from the prior pdf of each of the parameters (a parameter set) and calculates the likelihood of this set based on how well the model outputs calibrated to the observations. This process is iterated many times (40 000 times in our case), with the parameter set being stored along with the likelihood of this set. Phase two resamples these intermediate results to approximate the posterior pdf of each management indicator. The intermediate results were resampled, with the replacement using a probability based on the importance function. In our case, the joint prior pdf was used as the importance function (McAllister et al. 1994; Raftery et al. 1995), which meant that the resampling was proportional to the likelihood of each parameter set. Thus, with the prior pdf as the importance function, the greater the likelihood of a parameter set the more frequently this set would be resampled and included within the posterior. For a more detailed explanation of Bayesian SIR methods, see McAllister et al. (1994) and Punt and Hilborn (1997).

The likelihood function assumed that the observed catch was normally distributed about the predicted values, with a standard deviation . Thus, the log-likelihood (LL) for a given fishery's observations was proportional to (Haddon 2001):

$$LL^X = -\frac{n}{2}\left[Ln(2f) + 2Ln(\dagger^X) + 1\right] \text{, (23)}$$

$$\dagger^X = \sqrt{\sum_{t=1984-07}^{2005-06} \frac{\left(C_t^X - \hat{C}_t^X\right)}{2n}} \text{, (24)}$$

where X is the fishery (EPT or OPT), n is the number of data points, C_t^X is the observed catch for fishery X at month t, and $\hat{C}_t^X$ is the estimated catch from the model for fishery X at month t, with 1984–2007 and 2005–2006 representing the year–month limits of the observations.

The total log-likelihood for a single model run was then calculated as the sum of the log likelihoods for the ocean and estuary trawl fisheries:

$$LL = LL^{EPT} + LL^{OPT} \text{. (25)}$$

Only the OPT and EPT fisheries were included in the total log-likelihood because they represented the majority of the catch.

A joint posterior probability distribution for the key parameters was produced on the basis of the calculated log-likelihood for each model run (as described above). The quality of the posterior was determined on the basis of the efficiency of the importance function in the SIR method, as estimated using the maximum importance ratio (MIR) (McAllister and Pikitch 1997). The MIR is equal to the ratio of the maximum of likelihoods to the sum over all likelihoods. McAllister and Pikitch (1997) found that a maximum importance ratio of 0.04 "… appeared to provide estimates of posterior pdfs sufficiently precise for stock assessment and

decision analysis". Another means of improving the posterior pdf is to ensure that a single parameter set (the maximum single density MSD) is not assigned more than 1% of the total probability (Punt and Hilborn 1997).

The key parameters chosen for the Bayesian SIR calibration process were catchability (q), larval and juvenile mortality (LM and JM), and the two stock recruitment parameters (z and Rv). These were chosen as they were the parameters for which there was significant uncertainty regarding their true value (see Table 1) and they had the most effect on the management indicators in the sensitivity analysis. Parameters such as base unfished-zone salinity levels (C1SalBas) and unfished-zone and estuary food levels (C1FooBas and C2FooBas) were not chosen because they were surrogates for the impact of river discharge on the growth and movement of prawns and the uncertainty in this impact is captured to an extent in the stochasticity built into future river discharge and the various climate-change scenarios.

Calibration data and parameter values

Table 1. The initial values and references for the main parameters used in the calibration of this model

Data and parameter values	Sources
Catch and Effort data for 3 fisheries. Standard deviation of observed catch data used in Equation 3-20: 27,597 for EPT, 22,656 for OPT, and 6,240 for SPN.	NSW DPI ComCatch database based on monthly logsheets supplied by fishers.[A]
Clarence River discharge data	NSW Department of Natural Resources (2007)
Instantaneous adult mortality = 0.37 month^{-1}	Montgomery, S. (unpubl. data) Limits based on calibrating average prawn weights in EPT catch with estimates provided in Broadhurst et al. (2004).
Instantaneous larval mortality – Bayesian prior with uniform distribution between 2 and 4 month^{-1}.	
Instantaneous juvenile mortality = – Bayesian prior with uniform distribution between 50% and 100% of larval mortality.	
Migration parameters (e.g. LMov2_1 , JMov1_2, AMov2_3)	Initial values based on known movement patterns with larva migrating from the ocean to the estuary and unfished zone; juveniles migrating from the unfished zone to estuary; and adults migrating out of the unfished zone and estuary to the ocean (Glaister 1978b; Coles and Greenwood 1983)
Fecundity F1-F4 (0–20 mm CL) = 0, F5 (20–25 mm CL) = 3400, F6 (25–30 mm CL) = 4200, F7 (30–35 mm CL) = 5300, F8 (>35mm CL) = 6500 eggs month^{-1}	Equates to approx 230 000 eggs per female, which is in the range for other Metepenaeus species (Penn 1980; Dall et al. 1990, 7.1) with size class spread based on weight (Garcia and Le Reste 1981)
Average female growth L∞ = 37.41, K = 0.24 month^{-1}, t_0=0.7, Average male growth L∞ = 23.61, K = 0.70 month^{-1}, t_0=0.8, each growth group was spaced so that each had an L∞ that was 0.5 mm different from its neighbouring groups.	(Glaister 1977, p. 74)
Catchability (q) – Bayesian prior with uniform distribution between 0.0001 and 0.001.	(Coles and Greenwood 1983; Penn 1984; Broadhurst et al. 2004).
Virgin recruitment (Rv) – Bayesian prior with uniform distribution between 10e9 and 10e11.	Limits based on manual experimentation comparing changes in maximum likelihood with changes in Rv.
Slope of stock recruitment relationship (z) – Bayesian prior with uniform distribution between 0.2 and 0.7.	Relationship suggested by the work of (Ye 2000). Lower values reflecting the strength of the stock-recruitment relationship given that the model area covers the full migratory range of the Clarence River school prawn stock (Ruello 1977).
Change in catchability (dq) = 0.0004	O'Neill et al. (2003: table 6.4.4)
Weight for both sexes was calculated as: $\ln(w) = 2.917 \cdot \ln(l) - 6.919$, where w is weight (g) and l is carapace length (mm).	Broadhurst et al. (2004)
Gear selectivity: estuary and ocean prawn trawl: 40-mm diamond codend, L50 = 10.59, SR = 3.42	Macbeth et al. (2004)
Gear selectivity: Stow Netting, 30-mm diamond mesh codend, L50 = 8.46, SR=3.55	Macbeth et al. (2005)

Recruitment error (re) was taken from a log normal distribution with mean 0, coefficient of variation 0.2	Found to incorporate sufficient recruitment uncertainty for a similar peneaid species (*Melicertus plebejus*) (Ives and Scandol 2007)
Water temperature levels, approximated by a sine curve Cos(month / phase - freq)^ 2) * amp + base, with values of: C1: base 13°, amplitude 13°, frequency 3.8 and phase 3.5. C2: base 15°, amplitude 13°, frequency 3.8 and phase 3.5. C3: base 17°, amplitude 7°, frequency 3.8 and phase 3.5.	Taken from temperature loggers in Clarence River and data provided by Australian Bureau of Meteorology.
Salinity movement effect factor ([A]) = 1.01, Salinity Base Levels (sa_b^A): C1SalBas = 50, C2SalBas = 2300, C3SalBas = 35 000	Clarence Valley Council Floodplain Services (2006)
Food availability growth effect factor ([A]) = 1.01, base salinity levels (sa_b^A): C1FooBas = 100, C2FooBas = 100, C3FooBas = 90.	Chosen to calibrate the model.
Future river discharge estimates (L20D discharge mean and L20D discharge CV)	Based on the range of estimated % change in precipitation for the Clarence River Basin (152–154°E longitude and 29–30°S latitude) provided by the OzClim package (CSIRO and IGCI 2007)
River discharge event level (D_E) = 300 000 ML	Chosen to calibrate high catch levels associated with extreme maximum river discharge events. This level was exceeded only 6 times during the calibration period (1985–2005).

[A]Catch rate data were not standardised using generalised linear models (Hilborn and Walters 1992). However, a number of key issues traditionally addressed by standardisation were accounted for in this model. First, changes in fishing power over time, which can affect the validity of CPUE as an index of abundance, were dealt with by including a parameter for growth in catchability over time that was based on the standardisation work undertaken in Queensland (O'Neill *et al.* 2003). Second, seasonality in catchability, which can affect within year CPUE, was dealt with through the use of two additional parameters that fitted a seasonal pattern to catchability. These additional parameters therefore effectively altered the effect of the catch data on the model in the same way that data standardisation would have. By including these phenomena in the model, we are able to incorporate them in the sensitivity analysis and thereby analyse their importance as a driver of the management indicators.

References

Arhonditsis, G. B., and Brett, M. T. (2004). Evaluation of the current state of mechanistic aquatic biogeochemical modeling. Marine Ecology Progress Series 271, 13–26.

Aumann, C. A. (2007). A methodology for developing simulation models of complex systems. Ecological Modelling 202, 385–396.

Bagenal, T. B. (1973). Fish fecundity and its relations with stock and recruitment. Rapports et Proce`s-Verbaux des Re´unions du Conseil International pour l'Exploration de la Mer. 164, 186–198.

Broadhurst, M. K., Millar, R. B., Kennelly, S. J., Macbeth, W. G., Young, D. J., et al. (2004). Selectivity of conventional diamond- and novel square-mesh codends in an Australian estuarine penaeid-trawl fishery. Fisheries Research 67, 183–194.

Coles, R. G., and Greenwood, J. G. (1983). Seasonal movement and size distribution of three commercially important Australian prawn species (Crustacea: Penaeidae) within an estuarine system. Australian Journal of Marine and Freshwater Research 34, 727–743.

CSIRO & IGCI (2007) OzClim. (International Global Change Institute (IGCI), University of Waikato and CSIRO Atmospheric Research: Hobart, Tasmania)

Dall, W., Hill, B. J., Rothlisberg, P. C., and Sharples, D. J. (1990). 'The Biology of the Penaeidae.' (Academic Press: London.)

Drinkwater, K. F., Tremblay, M. J., and Comeau, M. (2006). The influence of wind and temperature on the catch rate of the American lobster (Homarus americanus) during spring fisheries off eastern Canada. Fisheries Oceanography 15, 150–165.

Garcia, S., and Le Reste, L. (1981). 'Life Cycles, Dynamics, Exploitation and Management of Coastal Penaeid Shrimp Stocks.' (Food and Agriculture Orgainization of the United Nations: Rome.)

Glaister, J. P. (1977) Ecological studies of Metapenaeus macleayi (Haswell) (Crustacean, Decapoda, Penaeidae) in Clarence river region, northern New South Wales. University of New England., Armidale

Glaister, J. P. (1978a). Impact of river discharge on distribution and production of the school prawn Metapenaeus macleayi (Haswell) (Crustacea: Penaeidae) in the Clarence river region, northern New South Wales. Australian Journal of Marine and Freshwater Research 38, 225–241.

Glaister, J. P. (1978b). Movement and growth of tagged school prawns, Metapenaeus macleayi (Haswell) (Crustacea: Penaeidae), in the Clarence River region of northern New South Wales. Australian Journal of Marine and Freshwater Research 29, 645–657.

Haddon, M. (2001). 'Modelling and Quantitative Methods in Fisheries.' (Chapman and Hall/CRC: London.)

Hilborn, R. and Walters, C. J. (1992). 'Quantitative Fisheries Stock Assessment: Choice, Dynamics and Uncertainty.' (Chapman and Hall: New York, NY).

Ives, M. C. and Scandol, J. P. (2007). A Bayesian analysis of NSW eastern king prawn stocks (Melicertus plebejus) using multiple model structures. Fisheries Research 84, 314-327.

Jones, A. R. (1987). Temporal patterns in the macrobenthic communities of the Hawkesbury estuary, New South Wales. Australian Journal of Marine and Freshwater Research 38, 607–624.

Kailola, P., Williams, M., Stewart, P., Russell, R., McNee, A., et al. (1993). 'Australian Fisheries Resources.' (Bureau of Resource Sciences and Fisheries Research and Development Corp.: Canberra.)

Kleijnen, J. P. C. (1995). Sensitivity analysis and related analyses: a survey of statistical techniques. In 'International Symposium SAMO95, Theory and applications of Sensitivity Analysis of Model Output in computer simulations'. (European Commission RTD Action Energy and Joint Research Centre, Belgirate, Italy)

Koeller, P. (1999). Influence of temperature and effort on lobster catches at different temporal and spatial scales and the implications for stock assessments. Fishery Bulletin 97, 62–70.

Macbeth, W. G., Broadhurst, M. K. and Millar, R. B. (2004). The utility of square mesh to reduce bycatch in Hawkesbury River prawn trawls. Ecological Management and Restoration 5, 221-224.

Macbeth, W. G., Broadhurst, M. K. and Millar, R. B. (2005). Improving selectivity in an Australian penaeid stow-net fishery. Bulletin of Marine Science 76, 647–660.

Mahevas, S., and Pelletier, D. (2004). ISIS–Fish, a generic and spatially explicit simulation tool for evaluating the impact of management measures on fisheries dynamics. Ecological Modelling 171, 65–84.

McAllister, M. K., and Pikitch, E. K. (1997). A Bayesian approach to choosing a design for surveying fishery resources: application to the eastern Bering Sea trawl survey. Canadian Journal of Fisheries and Aquatic Sciences 54, 301–311.

McAllister, M. K., Pikitch, E. K., Punt, A. E., and Hilborn, R. (1994). A Bayesian Approach to Stock Assessment and Harvest Decisions Using the Sampling/Importance Resampling Algorithm. Canadian Journal of Fisheries and Aquatic Sciences 51, 2673–2687.

Moll, A. (2000). Assessment of three-dimensional physical–biological ECOHAM1 simulations by quantified validation for the North Sea with ICES and ERSEM data. ICES Journal of Marine Science 57, 1060–1068.

Moore, S. K., Baird, M. E., and Suthers, I. M. (2006). Relative impacts of physical and biological processes on nutrient and phytoplankton dynamics in a shallow estuary after a storm event. Estuaries and Coasts 29, 81–95.

NSW Department of Natural Resources (2007). NSW Provisional River Data. NSW Department of Natural Resources. http://waterinfo.nsw.gov.au/river-provisional-sites.shtml

Neuheimer, A. B., and Taggart, C. T. (2007). The growing degree-day and fish size-at-age: the overlooked metric. Canadian Journal of Fisheries and Aquatic Sciences 64, 378–385.

O'Neill, M. F., Courtney, A. J., Turnbull, C. T., Good, N. M., Yeomans, K. M., et al. (2003). Comparison of relative fishing power between different sectors of the Queensland trawl fishery, Australia. Fisheries Research 65, 309-321.Penn, J. W. (1980). Spawning and fecundity of the western king prawn, Penaeus latisulcatus (Kishinouye), in Western Australian waters. Australian Journal of Marine and Freshwater Research 31, 21–35.

<enn, J. W. (1984). The behavior and catchability of some commercially exploited penaeids and their relationship to stock and recruitment. In 'Penaeid shrimps – Their Biology and Management'. (Eds J. A. Gulland and B. J. Rothschild.) pp. 173–186. (Fishing News Books Ltd: Surrey, England.)

Potter, I. C., Baronie, F. M., Manning, R. J. G., and Loneragan, N. R. (1989). Reproductive biology and growth of the western school prawn, Metapenaeus dalli, in a large Western Australian estuary. Australian Journal of Marine and Freshwater Research 40, 327–340.

Potter, I. C., Penn, J. W., and Brooker, K. S. (1986). Life cycle of the western school prawn, Metapenaeus dalli (Racek), in a Western Australian estuary. Australian Journal of Marine and Freshwater Research 37, 95–103.

Prince, J. D., Loneragan, N., and Okey, T. A. (2008). Contraction of the banana prawn (Penaeus merguiensis) fishery of Albatross Bay in the Gulf of Carpentaria, Australia. Marine and Freshwater Research 59, 383–390.

Punt, A. E., Campbell, R. A., and Smith, A. D. M. (2001). Evaluating empirical indicators and reference points for fisheries management: application to the broadbill swordfish fishery off eastern Australia. Marine and Freshwater Research 52, 819–832.

Punt, A. E., and Hilborn, R. (1997). Fisheries stock assessment and decision analysis: the Bayesian approach. Reviews in Fish Biology and Fisheries 7, 35–63.

Racek, A. A. (1959). Prawn investigations in eastern Australia. Research Bulletin of the New South Wales Fisheries Station 6, 1–57.

Raftery, A. E., Givens, G. H., and Zeh, J. E. (1995). Inference from a deterministic population dynamics model for bowhead whales. Journal of the American Statistical Association 90, 402–416.

Robins, J. B., Halliday, I. A., Staunton-Smith, J., Mayer, D. G., and Sellin, M. J. (2005). Freshwater-flow requirements of estuarine fisheries in tropical Australia: a review of the state of knowledge and application of a suggested approach. Marine and Freshwater Research 56, 343–360.

Rothlisberg, P. C., and Church, J. A. (1993). Processes controlling the larval dispersal and postlarval recruitment of penaeid prawns. In 'Coastal and Estuarine Studies'. (Eds P. W. Sammarco and M. L. Heron.) pp. 235–252. (American Geophysical Union: Washington, DC.)

Ruello, N. V. (1973a). Burrowing, feeding, and spatial distribution of the school prawn Metapenaeus macleayi (Haswell) in the Hunter river region, Australia. Journal of Experimental Marine Biology and Ecology 13, 189–206.

Ruello, N. V. (1973b). Influence of rainfall on the distribution and abundance of the school prawn Metapenaeus macleayi (Haswell) in the Hunter river region, Australia. Marine Biology 23, 221–228.

Ruello, N. V. (1977). Migration and stock studies on the Australian school prawn Metapenaeus macleayi. Marine Biology 41, 185-190.Somers, I. F. (1990). Manipulation of fishing effort in Australia's penaeid prawn fisheries. Australian Journal of Marine and Freshwater Research 41, 1–12.

Vance, D. J., Bishop, J., Dichmont, C. M., Hall, N., McInnes, K., et al. (2003). 'Management of Common Banana Prawn Stocks of the Gulf of Carpentaria: Separating the Effects of Fishing from those of the Environment.' (CSIRO, AFMA, Canberra.)

Walters, C., and Martell, J. D. (2004). 'Fisheries Ecology and Management.' (Princeton University Press: Princeton, NJ.)

Werner, E. E., and Gilliam, J. F. (1984). The ontogenetic niche and species interactions in size-structured populations. Annual Review of Ecology and Systematics 15, 393–425.

Wileman, D. A., Ferro, R. S. T., Fonteyne, R., and Millar, R. B. (1996). Manual of methods of measuring the selectivity of towed fishing gears. International Council for the Exploration of the Sea, Copenhagen, Denmark.

Ye, Y. (2000). Is recruitment related to spawning stock in penaeid shrimp fisheries? ICES Journal of Marine Science 57, 1103–1109.

Zhou, S., Dichmont, C., Burridge, C. Y., Venables, W. N., Toscas, P. J., et al. (2007). Is catchability density-dependent for schooling prawns? Fisheries Research 85, 23–36.