A spatial representation of the tiger prawn (*Penaeus esculentus*) fishery in Shark Bay, Western Australia

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Abstract

The fishery for brown tiger prawns, Penaeus esculentus, *in Shark Bay, Western Australia, experienced reduced recruitment in the early 1980s. It is considered that this decline resulted from recruitment overfishing. The measures subsequently implemented to reduce fishing effort on the tiger prawns were constrained by the objective of maintaining the harvest of western king prawns,* P. latisulcatus, *which was the dominant species in the catch. A series of spatial closures was applied to different regions within the fishery in an attempt to reduce effort on brown tiger prawns, yet maintain catches of western king prawns. The closures were intended to take advantage of the spatial structure of the fishery and the migration that occurs between fishing grounds. Until now, a subjective approach has been used, in consultation with the fishing industry, in determining the appropriate closures. A compartmental delay-difference model has been developed to represent the spatial structure of the brown tiger prawn fishery and to describe the distribution of the prawns through consecutive months of the fishing season. In the absence of explicit information on the rates of migration between fishing grounds, the model represents the migration rates as parameters, and estimates these, together with catchability and recruitment parameters, from the observed monthly catch rates within the fishing grounds. Using this model, a more accurate time series of annual recruitment indices has been calculated for the Shark Bay tiger prawn stock.*

Introduction

Commercial exploitation of prawns in Shark Bay (Figure 1) commenced in 1962. The two species that dominate the prawn catch in this fishery are western king prawns, *Penaeus latisulcatus,* and brown tiger prawns, *Penaeus esculentus*. Endeavour prawns, *Metapenaeus endeavouri*, and other smaller prawns are also caught as bycatch. Limited entry was introduced in 1963 and the fishing fleet was restricted to 25 trawlers (Penn *et al.* 1989). By 1975, the fleet had increased to 35 vessels (Penn *et al.* 1989), remaining at this level until 1990 when a buy-back programme reduced the number of vessels to 27.

Postlarval and early juvenile tiger prawns are found in *Posidonia* seagrass beds along the eastern and southern shorelines of Shark Bay (Penn and Stalker 1979). Larger juveniles (to 25 mm carapace length) are located along the seaward edges of the seagrass beds in water depths of 12-15 m, with nursery areas extending along both the eastern and southern shorelines (Penn 1988). Recruitment of juveniles to the trawl grounds begins in February-March of each year (Penn 1988). The Quobba, Western Ground, Elbow Shoals and Peron regions (Figure 1) were considered by Penn (1988) to have been equally important as recruitment areas. The average size of the tiger prawns in survey data increases to the west and north (Penn and Stalker 1979). While Slack-Smith (1969) suggested that tiger prawns moved northward, Penn (1988) noted that peak catches for regions other than Peron tended to occur in the same month of each year, and considered that the prawns at Peron were being fished earlier in their life cycle.

Initial assessments of the tiger prawn stock in Shark Bay were based on surplus production models (Hancock 1975; Bowen and Hancock 1984; Penn *et al.* 1989). These models were fitted to the total annual catch and effective effort for the stock, treating the fishery as a single spatial unit. Effective effort for each fishing season was calculated by dividing the annual catch by the average catch rate over fishing grounds and over months, using the method described by Hall and Penn (1979). Later assessments of the tiger prawn stock (Penn *et al.* 1989) have indicated that current levels of fishing effort are in excess of those that are associated with the peak of the stock production curve. Penn *et al.* (1989) expressed the view that surplus production models were no longer able to provide the advice required by managers of the Shark Bay prawn fishery, citing the lack of responsiveness of these models to recruitment overfishing and the need for information on the relationship between yield (or yield-per-recruit), fishing mortality and size-at-first-capture.

The decline in catches of tiger prawns in Shark Bay in the 1980s has been attributed to growth and recruitment overfishing (Penn *et al.* 1989). Although there was a need to rebuild the stock of tiger prawns, fisheries managers have been obliged to consider the potential impact of proposed rebuilding strategies on the catches of western king prawns, as this is the major species in the Shark Bay prawn fishery. The strategy that has been adopted to rebuild the tiger prawn stock has been to define areas where fishing is permitted. Fishing has been allowed in regions where king prawns are caught but catches of tiger prawns are reduced, while regions where exploitation of tiger prawns might be greater have been closed to fishing.

Early estimates of a recruitment index for Shark Bay tiger prawns were based on catch rates from the Western Ground (Figure 1) during March-May (Penn 1988). Later recruitment indices were derived using a simple cohort analysis. This assumed equivalence between growth and mortality. Recruitment was estimated from the weights of those catches recorded in fishing regions in which the new recruits were believed to be located (Penn *et al.* 1995).

Analysis of the fishery data for the prawn fisheries in Shark Bay has been complicated by the spatial structure of the fishery and the changing distribution of prawns and of fishing effort throughout the fishing season. The need existed for a spatial representation that provided a description of the fishery at monthly time steps. Walters (Prof. C. J. Walters, University of British Columbia, Canada, pers. comm.) developed a prototype age-structured spatial model of one of the prawn fisheries in Western Australia, which demonstrated that potentially such a model could be used for these fisheries.

The objective of this study was to develop a spatial model of the brown tiger prawn fishery of Shark Bay, in order to (1) describe the fishery at a spatial resolution consistent with current management strategies, (2) produce an improved time series of annual recruitment indices for the tiger prawn stock, and (3) estimate the proportions of prawns migrating between fishing regions.

Methods

Data used in the analysis

The data used for this study were the monthly records of catch (tonnes) and standardised fishing effort (thousand standard hours of trawling) within each of the fishing grounds in Shark Bay (Figure 1) for the annual fishing seasons from 1969 to 1980 and from 1982 to 1998.

Catch and nominal fishing effort data from the fishery have been collected through a comprehensive logbook programme which was initiated in the early 1960s

(Penn *et al.* 1989) and has subsequently operated in all years except 1981. An alternative data collection method was adopted for 1981, resulting in a break in the time series for that year. The logbook data have provided almost 100% coverage of catches from the fishery.

Information recorded within the logbooks consists of the fishers' estimates of the catch (kg) of each species obtained during each individual trawl, the duration (minutes) of trawling and the location of fishing. The location of fishing was originally recorded in the logbooks with reference to a 10' x 10' grid, based on latitude and longitude (Penn *et al.* 1989), but the logbook data recorded in this form have been reallocated to the fishing grounds that are now used to describe the fishery (Figure 1).

Accurate records of the landings by each vessel are obtained from the shore-based factories (Penn *et al.* 1989), or directly from those vessels that process their catches at sea. These have been used to adjust the logbook estimates of catch for errors of estimation, and to calculate values of any missing catch and effort data.

The vessels that now operate within the fishery have considerably greater fishing power than those that fished in earlier years (Penn *et al.* 1989). An estimate of the fishing power is calculated for each vessel, and such estimates are used to standardise the recorded fishing effort for each vessel within and between years (Hall and Penn 1979). The resulting estimates of standardised fishing effort represent the equivalent amount of fishing effort by a vessel with the average efficiency that existed in 1970.

Model

Time steps, t ($1 \le t \le 348$), used in the model were monthly, where $t=1$ represented January 1969. The year, y ($1969 \le y \le 1980$ or $1982 \le y \le 1998$), was calculated from the time step using the equation:

$$y = \begin{cases} 1969 + \text{int}\{(t-1)/12\} & \text{for } 1 \le t \le 144 \\ 1970 + \text{int}\{(t-1)/12\} & \text{for } 145 \le t \le 348 \end{cases} \quad (1)$$

while the calendar month, m ($1 \le m \le 12$), was calculated as

$$m = 1 + \{(t-1) \bmod 12\} \quad (2)$$

The function, int(x), returns the integer portion of the real number, x, truncating the decimal fraction. The function, j mod k, returns the remainder after the number j is divided by k.

The system state was represented in the model as a vector containing the number (thousands) of prawns, N_t^g, within each fishing ground, g ($1 \le g \le G$ where $G = 6$), at the beginning of the time-step, t, and a vector containing the biomass of prawns (tonnes) within each ground, B_t^g. The model does not differentiate between sexes of prawns. Codes used for the fishing grounds (Figure 1) were 1 = Quobba (Q), 2 = Koks Island (KI), 3 = Western Ground (WG), 4 = Elbow Shoals (ES), 5 = Peron (P) and 6 = West Peron (WP).

The model structure used to represent the fishery was based on the delay-difference model derived by Deriso (1980), which was subsequently extended by Schnute (1985, 1987), and described by Hilborn and Walters (1992). The equations representing the dynamics of the tiger prawn fishery were:

$$B_{t+1}^g = \sum_{j=1}^{G} \left\{ \left[\alpha N_t^j + \rho B_t^j \right] \left[1 - H_t^j \right] X_{j,g} \exp(-M) \right\} + W_R R_{t+1}^g \quad (3)$$

and

$$N_{t+1}^g = \sum_{j=1}^{G} \left\{ N_t^j \left[1 - H_t^j \right] X_{j,g} \exp(-M) \right\} + R_{t+1}^g \quad (4)$$

M is the instantaneous coefficient of natural mortality (month^{-1}). Growth was represented by the Brody growth equation, where the body weight (kg) of a prawn at time step t+1, w_{t+1}, was related to the weight at the previous monthly time step, w_t, by the equation

$$w_{t+1} = \alpha + \rho w_t \tag{5}$$

W_R is the body weight (kg) of a prawn at the age of recruitment to the exploited stock. The harvest rate (proportion caught) within fishing ground, g, at time step, t, is H_t^g. The proportion of prawns migrating from fishing ground j to fishing ground g at the end of the time step is $X_{j,g}$. The number (thousands) of prawns recruiting to fishing ground g at time step t is R_t^g.

Logbook data were not available for the Shark Bay fishery in 1981. It was assumed that the abundances (number and biomass) in the different fishing grounds at the commencement of 1982 were identical to those at the beginning of 1981.

No estimate was available for the instantaneous rate of natural mortality (M) for brown tiger prawns. Somers and Wang (1997) assumed $M = 0.18$ month^{-1}, and considered values ranging from 0.12 to 0.26 month^{-1} when assessing the sensitivity of their model for tiger prawns in Australia's northern prawn fishery. After reviewing estimates reported in the scientific literature, Garcia (1985) recorded that the reported level of M for adults of *Penaeus* species was around 0.2 month^{-1}. This latter value was applied for Shark Bay tiger prawns.

The weight (kg)-carapace length (mm) relationship (Penn and Hall 1974) for brown tiger prawns has been estimated as:

$$W = \begin{cases} 0.000002078L^{2.764} & \text{for males} \\ 0.000003739L^{2.574} & \text{for females} \end{cases} \tag{6}$$

It was assumed that male and female prawns recruit to the fishery at 20 mm carapace length, or a weight of approximately 0.0083 kg.

To reduce the number of parameters that were required to be estimated when fitting the model, estimates of the growth parameters were determined from the weight-length relationship (equation 6) and from parameters of the von Bertalanffy growth equations for *P. esculentus* reported in other studies (Kirkwood and Somers 1984; Wang and Somers 1996; Wang 1998). Approximate values of α and ρ were estimated as 0.0082 kg and 0.844 respectively.

The model was conditioned on catch (Punt 1988). The monthly harvest rate applied at each time step was calculated from the weight (tonnes) of the recorded catch, C_t^g, within the fishing ground for the time step, using the equation:

$$H_t^g = \frac{C_t^g}{B_t^g} \tag{7}$$

Using this estimate of harvest rate, an estimate of the number of prawns (thousands) caught within fishing ground g during time step t was calculated as $H_t^g N_t^g$. These estimates of catch in numbers were accumulated over all fishing grounds and months within the calendar year to obtain an estimate of the total annual catch in numbers, A_y.

The monthly harvest rate for a region was set to 1 when the weight of the recorded catch exceeded the estimated biomass that was available. A penalty function, λ_1, was applied when fitting to ensure that the harvest rate ranged between 0 and 1, where

$$\lambda_{t,1}^g = \begin{cases} 0 & \text{if } C_t^g \le B_t^g \\ 1000\left(C_t^g - B_t^g\right)^2 & \text{if } C_t^g > B_t^g \end{cases} \tag{8}$$

and

$$\lambda_1 = \sum_{t=1}^{348} \sum_{g=1}^{6} \lambda_{t,1}^g \tag{9}$$

The factor 1000 in equation (8) was chosen arbitrarily, but appeared adequate to ensure that parameter estimates resulted in an estimate of the biomass for each fishing region and time step that was sufficient to produce the recorded monthly catch.

The observed catch rate (kg/hour of trawling) was determined from the observed catch and standardised fishing effort, E_t^g, as

$$U_t^g = \frac{C_t^g}{E_t^g} \qquad (10)$$

while the expected catch rate, $\hat{U}_t^g$, was estimated as

$$\hat{U}_t^g = q^g B_t^g \qquad (11)$$

It was assumed that the catchability, q^g, within each fishing ground, g, remained constant over time (month and year).

The annual recruitment (thousands of prawns) to the whole fishery in calendar year, y, was denoted by R_y. It was assumed that the distribution of the relative recruitment within the calendar months of the year remained constant through time, where the proportion of the annual recruitment that recruited to the exploited stock in month m was denoted by p_m. Because of the limited catch and effort data available for November and December, it was assumed that $p_{11} = 0$ and $p_{12} = 0$, hence $p_{10} = 1 - \sum_{m=1}^{9} p_m$. It was also assumed that the relative distribution of recruitment to the different fishing grounds remained constant over time (month and year). The proportion of the recruitment for each month that recruits to fishing ground g was denoted by p^g, where $p^6 = 1 - \sum_{g=1}^{5} p^g$

The number of prawns, R_t^g, recruiting to the exploited stock within the fishing ground g at time step t was calculated from the annual recruitment, the proportion recruiting within the month and the proportion recruiting to the fishing ground:

$$R_t^g = p^g p_m R_y \qquad (12)$$

An alternative more complex model was also fitted, where the proportion recruiting to each fishing ground was constant within each year, but varied between years. For this model, the annual recruitment to each fishing ground, R_y^g, was regarded as a parameter to be estimated, and

$$R_t^g = p_m R_y^g \qquad (13)$$

To avoid the possibility of the optimisation procedure converging to extremely large estimates of population size and improbably low estimates of exploitation rate, an additional penalty function, λ_2, was calculated:

$$\lambda_2 = \sum_{y=1969}^{y=1998} \lambda_{y,2} \qquad (14)$$

where

$$\lambda_{y,2} = \begin{cases} 0 & \text{if } y = 1981 \text{ or } \dfrac{A_y}{R_y} \geq h \\ 1000\left(h - \dfrac{A_y}{R_y}\right)^2 & \text{otherwise} \end{cases} \qquad (15)$$

The fraction, h, was termed the minimum annual harvest fraction. The factor 1000 was chosen arbitrarily, but appeared adequate to ensure that estimates of annual recruitment levels and levels of exploitation were reasonable, given the exploitation status of the fishery.

Garcia (1985) reviewed the available studies for penaeid stocks and concluded that F_{MSY} for these studies was around 1.6 ± 0.3 year^{-1}, compared with the mean value of M in the same papers, which was 2.4 ± 0.3 year^{-1}. The Shark Bay tiger prawn stock has been fully exploited since the early 1970s, and experienced recruitment overfishing in the early 1980s. Based on this, the minimum annual harvest fraction, h, for the Shark Bay tiger prawn stock was set at 0.2. To test whether this constraint acted as an informative prior which played a significant role in determining the final parameter estimates, the model was also fitted with $h = 0.1$, and the results were compared.

The proportion of the prawns, $X_{g',g}$, migrating from fishing ground g' to fishing ground g at the end of each time step was assumed to remain constant through time. Slack-Smith (1969) had suggested a northward movement of tiger prawns. Thus, it was assumed that prawns only move northward between adjacent regions. The only monthly flows, $X_{g',g}$, considered in this study were $X_{6,5}$ $X_{5,4}$ $X_{4,3}$ $X_{3,2}$ and $X_{2,1}$ (Figure 1). With such flow of prawns from a fishing ground to only one adjacent fishing ground, the proportion remaining within the fishing ground from which the prawns emigrated was calculated as

$$X_{g',g'} = 1 - X_{g',g} \tag{16}$$

The system was assumed to be at an unexploited equilibrium at the beginning of the first time-step, with annual recruitment, R^*, where

$$R^* = R_{1969} \tag{17}$$

To determine the abundance (number and biomass) within each fishing ground at the commencement of each simulation run, the number and biomass within each region was set to zero, and the model run (without fishing mortality) through each month for 30 calendar years. The resulting set of numbers and biomasses was taken as the initial state of the fishery at the beginning of January 1969.

Parameters estimated for the less complex model were q^g (for $1 \le g \le 6$), $X_{2,1}$ $X_{3,2}$ $X_{4,3}$ $X_{5,4}$ $X_{6,5}$, p_m (for $1 \le m \le 9$), p^g (for $1 \le g \le 5$), and R_y (for $1969 \le y \le 1980$ or $1982 \le y \le 1998$). A total of 54 parameters were estimated for this model. The parameters was estimated for the more complex model were q^g (for $1 \le g \le 6$), $X_{2,1}$ $X_{3,2}$ $X_{4,3}$ $X_{5,4}$ $X_{6,5}$, p_m (for $1 \le m \le 9$), and R_y^g (for $1 \le g \le 6$ and $1969 \le y \le 1980$ or $1982 \le y \le 1998$). A total of 194 parameters were estimated for the more complex model.

The objective function used in fitting the model was

$$SS_1 = \sum_{t=1}^{348} \sum_{g=1}^{g} \left[\log\left(U_t^g + 1\right) - \log\left(\hat{U}_t^g + 1\right)\right]^2 \tag{18}$$

Catch rates were unavailable when regions were not fished within the month, thus reducing the number of observations included in calculation of SS_1. The model was implemented in AD Model Builder (Fournier 1994), which provided estimates of the parameters and the associated variance-covariance matrix of parameter estimates. Other versions were implemented in Microsoft Visual Basic and Microsoft EXCEL, to verify model implementation.

A phased approach was adopted when fitting the model. For the simpler 54 parameter model, it was assumed in the initial phase of model fitting that relative recruitment to each region and the relative recruitment to each month (January to October) were equal (for regions or months, respectively), the annual recruitment was constant through time, migration rates were equal and approximate values for catchabilities might be calculated as

$$\hat{q}^g = \frac{1}{n} \sum_t \log\left(\frac{U_t^g + 1}{B_t^g + 1}\right) \tag{19}$$

where n is the number of observations.

The initial estimates of the proportions migrating were set to 0.5, and the initial estimate of annual recruitment was set to 500 million prawns. The model was then fitted to the tiger prawn data to estimate proportions migrating and annual recruitment. Using these resulting parameter estimates as the new starting values, the constraints were progressively removed and the model fitted at each new phase to obtain the next set of starting values. Constraints were relaxed by first estimating the relative regional recruitment, and then, in order, the relative monthly recruitment, annual levels of recruitment, regional migration rates, and finally the approximation used to estimate catchabilities was dropped, allowing AD Model Builder to estimate these parameters. An iterative fitting procedure was then applied, alternating between fixing the catchabilities and fixing the levels of annual recruitment. The catchabilities are nuisance parameters, and are highly correlated with the levels of annual recruitment.

A similar approach was applied for the more complex 194 parameter model.

Selection of the more appropriate of the two models, the simpler 54 parameter model and the more complex 194 parameter model, was determined after calculation and consideration of two criteria. Akaike's information criterion (Akaike 1969) was calculated for each model using the formula:

$$AIC = n\log\left(\frac{SS}{n}\right) + 2p \tag{20}$$

where p is the number of parameters and n is the number of observations. The Bayesian Information Criterion (Schwarz 1978) was also calculated, as

$$BIC = n\log\left(\frac{SS}{n}\right) + p\log(n) \tag{21}$$

These criteria may be used to determine the optimum model complexity, by ensuring that each criterion is not increased when incorporating additional parameters. However, the Akaike Information Criterion tends to accept the more complex model when n is large (Raftery 1986 as cited by Zabel 1996), and the Bayesian Information Criterion is considered more appropriate in such situations, when conclusions based on the two criteria differ.

After selecting the more appropriate of the two models, the selected model's performance was tested by using it to generate 10 sets of synthetic data using a set of known parameters. Catch rates were calculated as $\hat{U}_t^g \exp(0.6\varepsilon_t^g)$, where ε_t^g were assumed to be standard normal variates. If the resulting catch rate was negative, it was reset to zero. The monthly harvest rate was calculated as

$$H_t^g = \left(\frac{0.2(y-1960)}{5+(y-1960)}\right)\left(\frac{(U_t^g)^5}{2.5^5+(U_t^g)^5}\right) \tag{22}$$

This arbitrary function increases with year, while responding to changes in catch rate within each fishing season.

The model was fitted to each set of synthetic data. Model estimates were compared with the actual parameter values used to generate the synthetic data.

When presenting results, approximate confidence limits were generated for each parameter by adding and subtracting twice the estimated standard deviation to and from the parameter estimate. The standard deviations were estimated from the Hessian matrix by AD Model Builder (Fournier 1994). When the resulting values fell outside the range valid for that variable, the value was reset to the appropriate upper or lower limit of the range.

Results

Selection of model complexity

The simpler form of the model, with 54 parameters, 1504 observations and minimum annual harvest fraction $h = 0.2$, resulted in an AIC of -1604 and a BIC of -1317 ($SS_1 = 482$), while the more complex model, with 194 parameters, 1504 observations and minimum annual harvest fraction $h = 0.2$, produced an AIC of -1873 and a BIC of -1239 ($SS_1 = 334$). With 1504 observations, the conclusion drawn from the BIC is preferred. Thus the simpler model was considered the more appropriate representation of the Shark Bay tiger prawn data, and was used in subsequent analysis.

Model results

The model was fitted under the assumption that the minimum annual harvest fraction was 0.2. The resulting parameter estimates for the 54 parameter model are presented in Tables 1 to 5.

The estimated percentage migrating between West Peron and Peron was 28.9%, while larger emigration rates of 100% were estimated from the Western Ground to Koks Island and Koks Island to Quobba (Table 1; Figure 2). The magnitude of the estimated rate increased from the south to the north.

The fishery received 22.6% of the total annual recruitment in January, with the estimates increasing to 30.4% in February and peaking at 31.6% in March before declining to 10.4% in April (Table 2; Figure 3). The estimated percentage recruitment in the period from May to September was 0%, but increased to 5.0% in October.

A plot of the proportion recruiting to each region is presented in Figure 4. The Western Ground received the lowest recruitment (2.9%), while Peron received the highest (31.8%) (Table 3). West Peron (15.8%) received greater recruitment than Quobba (11.8%), but slightly less than Koks Island (17.3%).

West Peron produced the highest estimate of catchability, i.e. 0.094 (1000 standard trawl hours)$^{-1}$ (Table 3; Figure 5). This is likely to reflect the size of the fishing ground over which the fleet operates (Figure 1). However, the Western Ground produced an estimate for catchability of 0.085 (1000 standard trawl hours)$^{-1}$, only slightly lower than that of West Peron. The lowest estimate of 0.008 (1000 standard trawl hours)$^{-1}$ was recorded for Quobba.

The marked decline in annual recruitment in the early 1980s is evident in the recruitment estimates presented in Figure 6 (also Tables 4 and 5). From 1985, estimates of annual recruitment increased, reaching a peak of 190 million in 1995 before declining to 105 million by 1998.

Sensitivity associated with minimum annual harvest fraction

Fitting the simpler form of model, with 54 parameters, 1504 observations and minimum annual harvest fraction $h = 0.1$ (rather than $h = 0.2$) reduced the sum of squares to $SS_1 = 446$ (from $SS_1 = 482$).

Comparison of the parameter estimates for $h = 0.1$ and $h = 0.2$ (Tables 1 to 5) suggested that, as the minimum annual harvest rate was relaxed, catchability estimates decreased and estimates of annual recruitment increased by about 80%. The pattern of annual recruitment remained similar (correlation coefficient = 0.976). However, the catchability showed a greater decrease in the northern than southern regions, while the catchability at Elbow Shoals remained relatively unchanged.

The percentage of annual recruitment received at Quobba increased from 11.8 to 22.5%, while Elbow Shoals recruitment decreased from 20.3 to 10.1% as the constraint on minimum annual harvest rate was relaxed. There was little change in the monthly distribution of recruitment. A general increase in migration rates resulted from the change from $h = 0.2$ to $h = 0.1$.

Analysis of synthetic data

Results of the analysis of the synthetic data sets are presented in Tables 6 to 9. In general, there was close agreement between the average of the parameter estimates and the actual parameter used in generating the data. However, the percentage of the annual recruitment received at Quobba was overestimated on average (16.7% compared with 11.7%), while at Peron it was underestimated (24.0% compared with 31.9%) (Table 7). Estimates of these parameters were imprecise (coefficient of variation of 0.59 for Quobba and 0.28 for Peron). Catchabilities at Peron and West Peron were overestimated by 56 and 25%, respectively (Table 7). The imprecision of the estimates of catchability increased with location of the regions from north to south.

Discussion

For over a decade, management of the tiger prawn fishery in Shark Bay has been based on advice derived from models that have treated the fishery as a single spatial entity. The advice related to the impact of alternative regional closures was subjective. While the implementation of such closures affected the distribution of fishing and the catch rates achieved, the resulting change to catchability was ignored in these models. The new model provides a description of the spatial structure of the fishery that, for the first time, permits exploration of the impact of the controls that are actually used in the fishery, i.e. the use of regional closures to control exploitation of the brown tiger prawns. Further, the study has provided information on both the regional and temporal distribution of recruitment of brown tiger prawns to the fishery and provided estimates of the annual recruitment to the fishery. The recruitment indices that had been used in earlier studies of the stock-recruitment relationship for tiger prawns in Shark Bay were derived from a simple cohort analysis. The new recruitment indices are considered more accurate as they are based on more appropriate assumptions.

Estimates of the proportions of annual recruitment received in the regions were consistent with the view of Penn (1988) that Quobba, Elbow Shoals and the Peron regions (Figure 1) were important as recruitment areas. However, the model also suggested that the West Peron region was of equal importance to the Quobba and Koks Island regions, and that the Western Ground received relatively little recruitment. The latter region had been considered a relatively important recruitment area (Penn 1988), and catch rates from this region had been the basis of the recruitment indices used in early stock-recruitment studies (Penn *et al.* 1995).

Lack of catch and effort data in November and December prevented the proportions of tiger prawns recruiting in these months from being estimated. It must be recognised that estimates of the proportions recruiting in the months from January to October were conditional on the assumption that there was zero recruitment in November and December. The small recruitment (5%) in October and relatively large recruitment estimated for January (22.6%) suggest that the assumption of zero recruitment for November and December may be inappropriate.

A number of zero values of observed catch rate were recorded, for which the model estimates were non-zero (due to the structure of the model); the number of such points appeared insufficient to justify change in model structure to accommodate such data. However future studies should address this issue.

The absence of logbook data for 1981 complicated the analysis. It was assumed that the numbers and biomass of prawns present within each region at the commencement of 1982 were equal to the numbers and biomass of prawns within that region at the beginning of 1981. This assumption ignores the level of recruitment in 1981 and the catches that occurred in 1981. However, total catch data are available for 1981, and alternative assumptions might be considered in future analyses that could be more appropriate. For example, the monthly catches and monthly harvest rates within each region applying in 1980 and 1982 might be averaged and used within the model to improve the estimate of the system state at the commencement of 1982. Exclusion of the observations for 1982 when calculating the objective function, SS_1, might also be considered, as this would reduce the possible sensitivity of parameter estimates to the assumptions associated with the 1981 fishing season.

It should be noted that considerable residual variation exists after fitting the tiger prawn model. A detailed examination of residuals may suggest other opportunities for model improvement. Further model simplification appears possible, as recruitment between May and September appears negligible, and the small level of recruitment in October is likely to have little impact on the objective function. Considerable model simplification also appears possible through replacement of the estimates of the annual recruitment by values determined from a stock-recruitment relationship.

While analysis of the synthetic data sets suggests that the model is likely to recover the actual parameter estimates used when generating the data, this conclusion must be qualified by noting that the synthetic data were produced by the same model. All assumptions regarding model structure were therefore satisfied. When applying the model to the actual fishery data, sensitivity to failure of model assumptions and to lack of contrast in the data must be considered.

For the Shark Bay tiger prawn fishery, the catch and effort data appear inadequate to allow the absolute magnitude of recruitment to be accurately estimated. This is reflected in the improved fit and marked change in parameter estimates obtained when the minimum annual harvest fraction was reduced from $h = 0.2$ to $h = 0.1$. Further improvement in the sum of squares was obtained by removing this constraint entirely, with estimates of exceptionally high recruitment levels and low exploitation resulting from the fitting procedure. It appears that the model compensates for higher recruitment by a decrease in catchability (particularly in the northern regions), and an increase in migration rates, moving the prawns to the less frequently fished Quobba region (fewer observations). For the model with $h = 0.2$, it is possible that the low value estimated for the catchability at Quobba compared with the catchability estimates for other regions, coupled with the high migration rates estimated for the more northerly regions, may reflect an overestimate of recruitment levels and underestimate of the level of exploitation.

Knowledge of the distribution of prawns (that is, relative levels of catchability for the fishing regions) or migration rates may assist in improving parameter estimation. Additional constraints imposed on catchability, based on the area swept and the area of the fishing grounds, may also assist. Until such further studies are undertaken, estimates of annual recruitment may be considered only to be indices of recruitment strength rather than absolute estimates of abundance. The high correlation between the recruitment levels estimated for $h = 0.2$ and $h = 0.1$ supports the view that the estimates are likely to be relatively accurate indices of the levels of annual recruitment.

As with estimates of the absolute levels of annual recruitment, estimates of migration rates must be considered uncertain, as it is likely that these also may be biased. Thus, the third objective of the study, to estimate migration rates, has not yet been achieved.

Catchabilities used within the model are assumed to be dependent on the region, but constant over time (month and year). Following a study of the behaviour of prawns in aquaria, Penn (1988) concluded that, unlike western king prawns, Western Australian tiger prawns exhibited no major response to temperature changes and accordingly, vulnerability was likely to be relatively consistent. The model may need modification before it is applied to the western king prawn fisheries of Western Australia, in order to represent the seasonal changes in water temperature that affect the monthly catchabilities for this species.

This study has provided, for the first time, estimates of the proportion of recruitment of brown tiger prawns occurring in Shark Bay within each month. It has also produced indices of the annual recruitment of brown tiger prawns in the Shark Bay fishery, based on assumptions that are sounder than those used in earlier studies. The study has assisted in identifying research needs for the fishery and has provided managers of the Shark Bay tiger prawn fishery with a model that matches the spatial resolution of the strategies by which the fishery is currently managed. The model that has been developed will allow more detailed and informed evaluation of proposals for the future management of the Shark Bay tiger prawn fishery.

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Table 1. Estimates of migration for brown tiger prawns in Shark Bay.

Estimates of proportions migrating obtained by fitting the model to the fishery data when the minimum annual harvest fraction was set to either 0.2 or 0.1. Parameter estimates and approximate lower and upper 95% confidence intervals are presented. Regions are Quobba (Q), Koks Island (KI), Western Ground (WG), Elbow Shoals (ES), Peron (P), and West Peron (WP).

Source and desination regions	Min. harvest fraction = 0.2			Min. harvest fraction = 0.1		
	Estimate	Lower CL	Upper CL	Estimate	Lower CL	Upper CL
KI to Q	1.000	0.997	1.000	1.000	0.995	1.000
WG to KI	1.000	0.997	1.000	1.000	0.998	1.000
ES to WG	0.627	0.542	0.713	1.000	0.989	1.000
P to ES	0.338	0.284	0.392	0.410	0.365	0.455
WP to P	0.289	0.234	0.345	0.318	0.265	0.370

Table 2. Estimates of relative monthly recruitment parameters for brown tiger prawns in Shark Bay.

Estimates of proportions recruiting within each month obtained by fitting the model to the fishery data when the minimum annual harvest fraction was set to either 0.2 or 0.1. Parameter estimates and approximate lower and upper 95% confidence intervals are presented. The proportion recruiting in October may be calculated by subtracting from 1 the sum of the monthly proportions. Regions are Quobba (Q), Koks Island (KI), Western Ground (WG), Elbow Shoals (ES), Peron (P), and West Peron (WP).

	Min. harvest fraction = 0.2			Min. harvest fraction = 0.1		
Month	Estimate	Lower CL	Upper CL	Estimate	Lower CL	Upper CL
Jan	0.226	0.152	0.322	0.274	0.188	0.381
Feb	0.304	0.232	0.357	0.248	0.166	0.318
Mar	0.316	0.273	0.270	0.311	0.263	0.252
Apr	0.104	0.145	0.044	0.118	0.186	0.043
May	0.000	0.000	0.008	0.000	0.000	0.007
Jun	0.000	0.000	0.000	0.000	0.000	0.000
Jul	0.000	0.000	0.000	0.000	0.000	0.000
Aug	0.000	0.000	0.000	0.000	0.000	0.000
Sep	0.000	0.000	0.000	0.000	0.000	0.000

Table 3. Estimates of relative regional recruitment and catchability parameters for brown tiger prawns in Shark Bay.

Estimates of proportions recruiting to each region and catchabilities obtained by fitting the model to the fishery data when the minimum annual harvest fraction was set to either 0.2 or 0.1. Parameter estimates and approximate lower and upper 95% confidence intervals are presented. The proportion recruiting to West Peron may be calculated by subtracting from 1 the sum of the regional proportions. Regions are Quobba (Q), Koks Island (KI), Western Ground (WG), Elbow Shoals (ES), Peron (P), and West Peron (WP).

		Min. harvest fraction = 0.2			Min. harvest fraction = 0.1		
	Region	Estimate	Lower CL	Upper CL	Estimate	Lower CL	Upper CL
Regional recruitment proportion	Q	0.118	0.063	0.212	0.225	0.155	0.314
	KI	0.173	0.124	0.221	0.181	0.133	0.228
	WG	0.029	0.007	0.099	0.045	0.020	0.086
	ES	0.203	0.181	0.181	0.101	0.086	0.097
	P	0.318	0.366	0.213	0.321	0.388	0.214
Catchability	Q	0.008			0.004		
(1000 hours trawling)$^{-1}$	KI	0.065			0.035		
	WG	0.085			0.050		
	ES	0.053			0.051		
	P	0.039			0.025		
	WP	0.094			0.071		

Table 4. Estimated recruitment parameters for brown tiger prawns in Shark Bay from 1969 to 1984.

Estimates of annual recruitment (millions of prawns) obtained by fitting the model to the fishery data when the minimum annual harvest fraction is set to either 0.2 or 0.1. Parameter estimates and approximate lower and upper 95% confidence intervals are presented. No estimate is available for 1981.

	Min. harvest fraction = 0.2			Min. harvest fraction = 0.1		
Year	Estimate	Lower CL	Upper CL	Estimate	Lower CL	Upper CL
1969	142	115	170	309	239	379
1970	160	134	186	297	229	365
1971	103	81	126	179	133	225
1972	89	68	109	164	123	205
1973	147	118	176	281	220	342
1974	184	158	209	300	300	300
1975	169	143	196	300	299	301
1976	164	139	189	291	236	345
1977	130	107	153	239	192	287
1978	184	155	212	300	300	300
1979	165	141	188	276	227	326
1980	51	39	62	94	70	118

Table 5. Estimated recruitment parameters for brown tiger prawns in Shark Bay from 1985 to 1998.

Estimates of annual recruitment (millions of prawns) obtained by fitting the model to the fishery data when the minimum annual harvest fraction is set to either 0.2 or 0.1. Parameter estimates and approximate lower and upper 95% confidence intervals are presented.

	Min. harvest fraction = 0.2			Min. harvest fraction = 0.1		
Year	Estimate	Lower CL	Upper CL	Estimate	Lower CL	Upper CL
1985	49	39	59	85	64	106
1986	56	46	67	97	74	120
1987	49	38	59	85	63	106
1988	63	53	73	112	85	140
1989	71	60	82	135	102	168
1990	61	50	72	123	93	153
1991	94	79	109	182	145	220
1992	98	81	115	197	156	239
1993	84	70	99	167	130	203
1994	131	114	149	232	187	276
1995	190	170	210	300	300	300

Table 6. Estimates of migration and relative monthly recruitment parameters with actual parameters used to generate simulated data sets.

The actual parameters used to generate 10 sets of synthetic data, and the average, minimum, maximum, and lower and upper 95% confidence limits for the estimated parameters obtained when fitting the model to the simulated data. The proportion recruiting in October may be calculated by subtracting from 1 the sum of the monthly proportions. Regions are Quobba (Q), Koks Island (KI), Western Ground (WG), Elbow Shoals (ES), Peron (P), and West Peron (WP). Confidence levels for proportions were constrained to lie between 0 and 1.

	Regions or Month	Actual	Mean	Minimum	Maximum	Lower CL	Upper CL
Migration proportion	KI to Q	1.000	0.967	0.782	1.000	0.801	1.000
	WG to KI	1.000	0.916	0.811	1.000	0.740	1.000
	ES to WG	0.626	0.564	0.361	0.870	0.191	0.936
	P to ES	0.338	0.371	0.281	0.488	0.231	0.511
	WP to P	0.289	0.312	0.237	0.393	0.210	0.415
Monthly recruitment proportion	Jan	0.226	0.207	0.172	0.265	0.150	0.264
	Feb	0.305	0.275	0.235	0.321	0.210	0.340
	Mar	0.316	0.304	0.215	0.420	0.171	0.438
	Apr	0.102	0.118	0.000	0.173	0.000	0.245
	May	0.000	0.026	0.000	0.078	0.000	0.087
	Jun	0.000	0.013	0.000	0.048	0.000	0.054
	Jul	0.000	0.001	0.000	0.006	0.000	0.005
	Aug	0.000	0.005	0.000	0.019	0.000	0.021
	Sep	0.000	0.002	0.000	0.011	0.000	0.010

Table 7. Estimates of regional recruitment and catchability parameters with actual parameters used to generate simulated data sets.

The actual parameters used to generate 10 sets of synthetic data, and the average, minimum, maximum, and lower and upper 95% confidence limits for the estimated parameters obtained when fitting the model to the simulated data. The proportion recruiting to West Peron may be calculated by subtracting from 1 the sum of the regional proportions. Regions are Quobba (Q), Koks Island (KI), Western Ground (WG), Elbow Shoals (ES), Peron (P), and West Peron (WP). Confidence levels for proportions were constrained to lie between 0 and 1.

	Region	Actual	Mean	Minimum	Maximum	Lower CL	Upper CL
Regional recruitment proportion	Q	0.117	0.167	0.034	0.365	0.000	0.389
	KI	0.173	0.173	0.139	0.221	0.110	0.236
	WG	0.029	0.040	0.027	0.071	0.011	0.068
	ES	0.204	0.235	0.135	0.322	0.115	0.355
	P	0.319	0.240	0.135	0.357	0.085	0.395
Catchability	Q	0.008	0.008	0.003	0.012	0.002	0.015
$(1000 \text{ hours trawling})^{-1}$	KI	0.065	0.070	0.054	0.084	0.048	0.092
	WG	0.085	0.091	0.074	0.117	0.056	0.125
	ES	0.053	0.056	0.035	0.082	0.020	0.093
	P	0.039	0.061	0.033	0.093	0.018	0.104
	WP	0.094	0.117	0.089	0.171	0.058	0.176

Table 8. Estimates of recruitment (millions of prawns) from 1969 to 1984 with actual parameters used to generate simulated data sets.

The actual parameters used to generate 10 sets of synthetic data, and the average, minimum, maximum, and lower and upper 95% confidence limits for the estimated parameters obtained when fitting the model to the simulated data. No estimate is available for 1981.

Year	Actual	Mean	Minimum	Maximum	Lower CL	Upper CL
1969	142	147	126	210	89	206
1970	160	164	134	236	98	229
1971	103	108	88	154	60	155
1972	88	92	73	154	39	145
1973	147	153	131	238	80	225
1974	183	192	160	287	102	282
1975	169	176	144	264	95	258
1976	164	175	141	255	97	252
1977	129	142	115	225	68	216
1978	183	189	163	266	115	262
1979	164	173	145	256	98	248
1980	50	54	41	82	26	81
1982	58	62	49	97	29	96
1983	107	112	95	174	61	164
1984	74	79	66	121	39	118

Table 9. Estimates of recruitment (millions of prawns) from 1985 to 1998 with actual parameters used to generate simulated data sets.

The actual parameters used to generate 10 sets of synthetic data, and the average, minimum, maximum, and lower and upper 95% confidence limits for the estimated parameters obtained when fitting the model to the simulated data.

Year	Actual	Mean	Minimum	Maximum	Lower CL	Upper CL
1985	49	51	39	81	22	80
1986	56	61	45	93	30	92
1987	49	52	41	77	27	77
1988	63	66	56	96	36	96
1989	71	76	60	111	43	109
1990	61	63	51	88	35	90
1991	94	98	81	147	53	143
1992	98	106	88	160	55	156
1993	84	89	72	141	44	133
1994	131	138	116	209	74	202
1995	189	198	167	285	119	277
1996	138	146	119	215	80	212
1997	110	114	89	168	61	167
1998	105	110	94	172	56	164

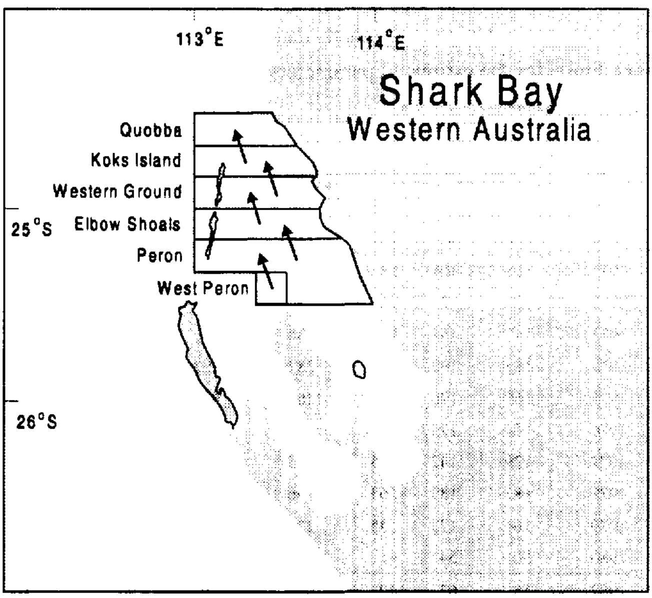

Figure 1. Fishing regions within the Shark Bay prawn fishery. Arrows indicate the migration assumed within the fishery model.

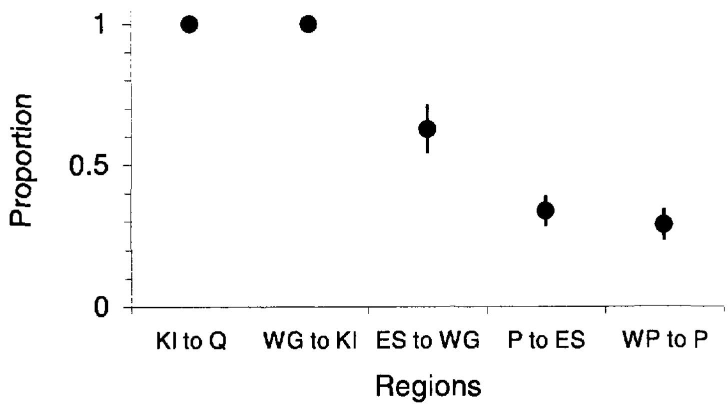

Figure 2. Estimated proportions of brown tiger prawns migrating each month between different fishing grounds in Shark Bay (Q=Quobba, KI=Koks Island, WG=Western Ground, ES=Elbow Shoals, P=Peron, and WP=West Peron). The error bars represent values between 0 and 1 lying within two standard deviations of the parameter estimates.

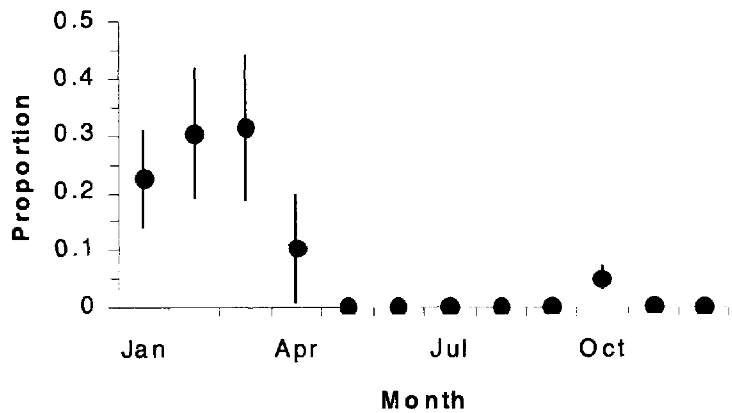

Figure 3. Estimated proportion of the recruitment of brown tiger prawns occurring within each calendar month in the Shark Bay fishery. The error bars represent

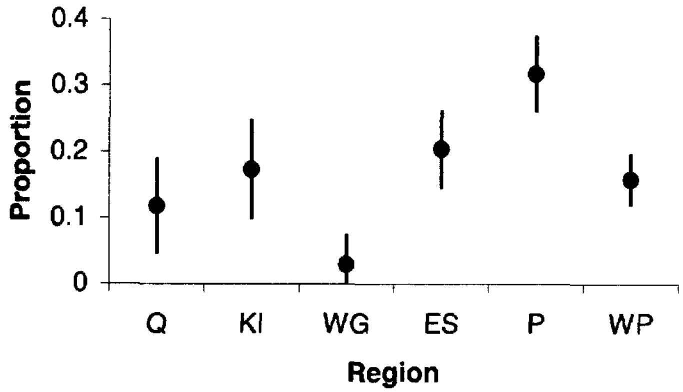

Figure 4. Estimated proportion of the recruitment of brown tiger prawns occurring within each region in the Shark Bay fishery (Q=Quobba, KI=Koks Island, WG=Western Ground, ES=Elbow Shoals, P=Peron, and WP=West Peron). The error bars represent positive values within two standard deviations of the parameter estimates.

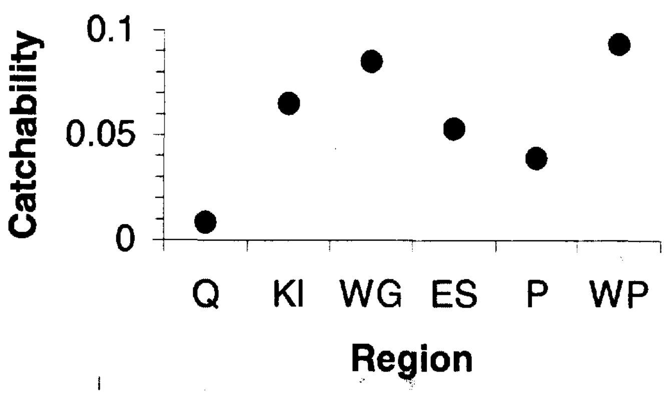

Figure 5. Estimated catchability of brown tiger prawns within different fishing regions of Shark Bay (Q=Quobba, KI=Koks Island, WG=Western Ground, ES=Elbow Shoals, P=Peron, and WP=West Peron).

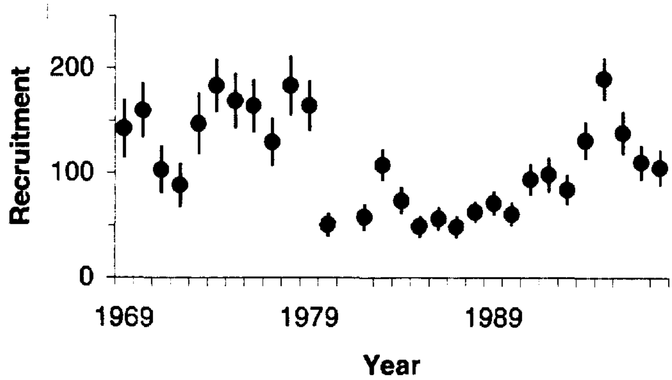

Figure 6. Estimated annual recruitment (millions of prawns) for the Shark Bay tiger prawn stock. The error bars represent values within two standard deviations of the parameter estimates.