

## A per-recruit simulation model for evaluating spatial closures in an Australian penaeid fishery

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### Abstract

Spatial closures are commonly used by Australian fisheries managers to alter fishing patterns. To evaluate different fishing closures, however, fishery scientists have to understand and model the spatio-temporal interactions between fish stocks and fishing fleets. We develop a deterministic, stationary, per-recruit, age-structured simulation model to assess different spatial closure strategies, and use data from the Torres Strait tiger prawn fishery, *Penaeus esculentus*, as a working example. Our results show that selection of an optimum spatial closure largely depends on the relative importance given to changes of the different utility functions evaluated (yield, value, egg production). We show that, on average, with a spatial closure yield-per-recruit would decrease, but also show that value-per-recruit may increase 10% with the appropriate closure. Our results suggest that egg-per-recruit would always increase in the presence of a closure. By incorporating parameter uncertainty within the simulation model we predict the uncertainty associated with alternative closure strategies, and thus provide valuable information for the decision-making process.

**Keywords:** Per-recruit analysis, fishery management, spatial modelling, *Penaeus esculentus*.

*Évaluation des zones de fermeture de pêche de pénéidés, en Australie, au moyen d'un modèle de simulation par recrue.*

### Résumé

L'administration des pêches australiennes utilise communément des zones de fermeture pour modifier la distribution de la pêche. Afin d'évaluer ces fermetures, les biologistes des pêches ont à connaître et à comprendre les interactions spatio-temporelles entre les stocks de crevettes et les flottes de pêche. Nous avons développé un modèle de simulation par recrue, structuré par âge, déterministe et stationnaire pour estimer différentes stratégies de zones de fermeture en utilisant comme exemple les données de pêche de *Penaeus esculentus* du détroit de Torres. Nos résultats montrent qu'une sélection de zone optimum de fermeture dépend largement de l'importance relative donnée aux changements des différentes fonctions évaluées (rendement, valeur, production d'œufs). Nous montrons qu'en moyenne, avec la fermeture d'une zone, le rendement par recrue diminuerait mais aussi que la valeur par recrue pourrait augmenter de 10 % avec une zone de fermeture appropriée. Nos résultats suggèrent que le nombre d'œufs par recrue augmente en la présence d'une fermeture. En incorporant des paramètres d'incertitude dans le modèle de simulation, nous prédisons l'incertitude associée aux stratégies alternatives de fermeture, fournissant ainsi des informations précieuses pour la prise de décision.

**Mots-clés :** Analyse par recrue, aménagement des pêches, modèle spatial, *Penaeus esculentus*.

## INTRODUCTION

Fisheries managers often rely on fishing closures to properly allocate, conserve and optimize the usage of natural resources. These closures modify the distribution of fishing effort in time and space and restrict fishers access to some components of the stock. It is the complex spatial and temporal interaction between fishing effort patterns and stock dynamics what will determine the success or failure of any closure strategy. In Australian tropical penaeid fisheries, fishing closures have been mainly used as a tool for harvest optimization.

Tropical penaeids grow rapidly, are short-lived, and are subject to high natural mortality. Their market value increases markedly with size, and given their fast growth may more than double in only a few months. To extract the maximum value from such stocks the time of harvest is critical. Therefore, to prevent growth overfishing, managers must isolate the under-sized components stocks from fishing effort. If recruitment periods are predictable and well-defined, seasonal closures offer an effective method of protecting such under-sized components of the stock. If, however, recruitment patterns are protracted, then under-sized components of a stock may only be spatially discernible, and can only be protected by spatial closures.

Previous studies of tropical penaeid fisheries have investigated seasonal closures. Some have employed computer modelling such as Dudley and Waugh (1980), Sluczanski (1984), Watson and Restrepo (in press), and Watson *et al.* [in press (a)] to explore the best seasonal fishing effort pattern which meets some management objective, usually catch value. Others such as Grey and Bukworth (1983) have examined whether small shrimp stocks were protected by specific closure periods. Little has been reported on the evaluation of spatial closures except for work done in the Gulf of Mexico (Nichols, 1983; Nance *et al.*, 1989) which compared 15 and 200 nautical mile closures off-shore from the state of Texas.

Shrimp fisheries in northern Australia extend along thousands of kilometres of coastline, from temperate to tropical latitudes. Most of these are multispecies fisheries which harvest several different species of shrimp depending on their geographical location. The various species exhibit different life-history parameters and their recruitment patterns vary considerably. This, combined with the presence of protracted recruitment, makes it difficult to protect small shrimp with seasonal closures.

Many studies have reported that small shrimp are strongly spatially stratified (Coles *et al.*, 1985; Courtney *et al.*, 1991). Thus spatial closures have often appeared as likely candidates for protecting small shrimp, and are used for that purpose throughout Australia. This study aims to develop a method for assessing a range of different closure strategies and

uses data from the Torres Strait shrimp fishery in northern Australia as an example.

## METHODS

### Simulation model

The model follows a utility-per-recruit approach (Die *et al.*, 1988), and is implemented as a discrete time simulation of the fishery system. Each month a group of animals (monthly cohort) is incorporated into the population. Individual growth is deterministic and animals within a monthly cohort have the same age and size.

The population is divided into two groups which occupy either the fished (open) or the unfished (closed) areas of the simulated fishery. Recruitment to the simulated population occurs only in the closed area, whereas animals become available to the fishery only after they migrate to the open area. In the model a net migration of animals occurs from the closed to the open areas.

Fishing effort in any given month is assumed to be a function of the accumulation of biomass in the fished grounds. The model is used to investigate several alternative spatial closure strategies by stepping through a vector of closure widths which represent the size of the closed area. The model calculates population numbers, catch, value of the catch and egg production at each time step (monthly) and provides per-recruit values when the stationary equilibrium is reached. Model components are presented in detail below and a notation list with definitions is given in *table 1*.

Let ( $i=1, 2 \dots 12$ ) denote the month of the year,  $j$  ( $j=1, 2 \dots 12$ ) be the cohort number,  $x$  (females,  $x=1$ , males,  $x=2$ ) be the animal's gender, and  $s$  ( $s=1$  in the closed area, and  $s=2$ , in the open area) be the population group. Mortality is represented by an exponential decline,

$$N_{j+1, j, x, 1} = (N_{i, j, x, 1} - D_{i, j, x}) e^{-Z_{i, j, x, 1}}, \quad (1a)$$

$$N_{j+1, j, x, 2} = N_{i, j, x, 2} e^{-Z_{i, j, x, 2}} + D_{i, j, x} e^{-Z_{i, j, x, 1}}, \quad (1b)$$

where  $N_{i, j, x, s}$  denotes the population numbers at the beginning of the month, where  $D_{i, j, x}$  is the number of migrants and where  $Z_{i, j, x, s}$  is the instantaneous coefficient of total mortality, given by

$$Z_{i, j, x, s} = M_{i, j, x} + F_{i, j, x, s} \quad (2)$$

Here,  $M_{i, j, x}$  and  $Z_{i, j, x, s}$  are the instantaneous coefficients of natural and fishing mortality respectively.  $F_{i, j, x, s}$  is calculated as,

$$F_{i, j, x, 2} = \frac{\varpi_i}{1 + e^{\gamma(L_{i, j, x} - \rho)}}, \quad (3)$$

**Table 1.** — Definitions of terms used in the simulation model of the effects of spatial closures in the Torres Strait fishery.

<i>a</i>	parameter in maturity function
<i>b</i>	parameter in maturity function
$C_{i,j,x}$	monthly catch
$D_{i,j,x}$	monthly migrants from the closed to the open area
$E_{i,j}$	monthly egg production
$F_{i,j,x,s}$	monthly instantaneous coefficient of fishing mortality
$F_{mult}$	fishing mortality multiplier
<i>g</i>	intercept of natural mortality-length function
<i>h</i>	intercept in length-fecundity function
<i>i</i>	month of simulation
<i>j</i>	cohort number (month)
<i>k</i>	coefficient of growth for von Bertalanffy function
$L_{i,j,x}$	carapace length (mm)
$L_{\infty}$	asymptotic length for von Bertalanffy growth function
<i>m</i>	slope of length-fecundity function
$M_{i,j,x}$	monthly instantaneous coefficient of natural mortality
$M_{mult}$	natural mortality multiplier
$N_{i,j,x,s}$	monthly population numbers
$N_{i,i,x,1}$	monthly recruitment numbers
$\bar{N}_{i,j,x,s}$	average monthly population size
$P_{i,j}$	proportion of mature females
$Q_{i,j}$	average individual fecundity of females
<i>s</i>	area (1 = closed, 2 = open)
<i>t</i>	age in months
<i>u</i>	slope of natural mortality-length function
$v_L$	value of commercial size <i>L</i>
$v_{i,j,x}$	individual value
$V_{i,j,x}$	monthly value of catch
$W_{i,j,x}$	mean weight of individuals
<i>x</i>	sex of animal (1 = females, 2 = males)
$Y_{i,j,x}$	monthly yield
$Z_{i,j,x,s}$	monthly instantaneous coefficient of total mortality
<i>E/R</i>	eggs-per-recruit
<i>V/R</i>	value-per-recruit
<i>Y/R</i>	yield-per-recruit
$\alpha$	multiplier parameter of weight-length function
$\beta_x$	residence time within the closed area
$\sigma_x$	standard error of the average residence time
$\gamma$	slope of the selectivity curve
$\delta$	closure width
$\varepsilon_x$	error term in residence time function
$\zeta_i$	monthly maximum proportion mature
$\theta_{i,x}$	probability of migration to open area
$\lambda_{t,x}$	cumulative probability of migration
$\mu_x$	reciprocal of migration speed
$\varphi$	exponential of weight-length function
$\omega_i$	monthly instantaneous fishing mortality coefficient of fully selected animals
$\rho$	length at 50% selection
$\tau_x$	age at recruitment
$\Omega_i$	monthly instantaneous fishing mortality coefficient in the absence of a closure

where  $\omega_i$  is the fishing mortality of fully selected animals,  $\gamma$  is the slope of the selectivity curve and  $\rho$  is the length at 50% selection. The fishing mortality in the closed area  $F_{i,j,x,1}$  is assumed to be zero. Natural mortality is assumed to be a decreasing function of size  $L_{i,j,x}$

$$M_{i,j,x} = ge^{-uL_{i,j,x}} \quad (4)$$

Sex-specific residence time  $\beta_x$  within the closed area is linear function of the width of this area  $\delta$ ,

$$\beta_x = \tau_x + \delta\mu_x + \varepsilon \quad (5)$$

Where  $\varepsilon$  is normally distributed  $N(0, \sigma_x)$ . Note that the reciprocal of  $\mu_x$  represents the migration speed. We believe that for most shrimp stocks the value of  $\varepsilon$  is quite large and can not be ignored. Because we assume that  $\varepsilon$  is a normally distributed error, then the cumulative probability of migration, from  $s=1$  to  $s=2$ ,  $\lambda_{t,x}$  becomes a cumulative normal function of age  $t$  and residence time  $\beta_x$ , which can be approximated with,

$$\lambda_{t,x} = \frac{1}{1 + e^{-((\beta_x - t)/\sigma_x)^2}} \quad (6)$$

where age is a function of month, cohort and the age at recruitment. Then, the probability that an animal migrates out of the closed area  $\theta_{t,x}$  is a function of its age  $t$  and the cumulative probability of migration,

$$\theta_{t,x} = \frac{\lambda_{t,x} - \lambda_{t-1,x}}{1 - \lambda_{t-1,x}} \quad (7)$$

Therefore, the number of migrants out of the closed area is a product of the above probability and the number of animals present in that area

$$D_{i,j,x} = \theta_{t,x} N_{i,j,x,1} \quad (8)$$

The monthly fishing mortality of fully selected animals is a function of the accumulation of biomass within the open area, itself a complicated function of the recruitment, migration, growth and mortality rates. Herein, for simplicity, it is assumed that fishing mortality of fully selected animals can be approximated with the observed fishing mortality pattern in the absence of a closure  $\Omega$ , lagged by the residence time  $\beta$ ,

$$\omega_i = \Omega_{i-\beta} \quad (9)$$

where the residence time is averaged between sexes,

$$\beta = \frac{\beta_1 + \beta_2}{2} \quad (10)$$

Average monthly population sizes are then given by

$$\bar{N}_{i,j,x,s} = N_{i,j,x,s} \frac{1 - e^{-Z_{i,j,x,s}}}{Z_{i,j,x,s}} \quad (11)$$

and monthly catch is given by

$$C_{i,j,x} = F_{i,j,x,2} \bar{N}_{i,j,x,2} \quad (12)$$

Growth follows a von Bertalanffy equation and the average monthly carapace lengths for each cohort are approximated with the value of length in the middle

**Table 2.** – Biological and fishery parameters used for a simulation of the effects of spatial closures in the Torres Strait fishery (parameter symbols as in table 1).

Mortality												
Month ( <i>i</i> )												
	1	2	3	4	5	6	7	8	9	10	11	12
$\Omega$	0.09	0.28	0.41	0.24	0.28	0.21	0.22	0.22	0.22	0.14	0.08	0.02
$g = 0.46$ $u = 0.027$ $\rho = 21.5$ (mm) $\gamma = 0.3$ (mm) $M_{\text{mult}} = 0.75, 0.8, 0.85 \dots 1.25$ $F_{\text{mult}} = 0.75, 0.8, 0.85 \dots 1.25$												
Migration and Recruitment												
Month ( <i>i</i> )												
	1	2	3	4	5	6	7	8	9	10	11	12
$N_{i,j,x,i}$	0.08	0.04	0.08	0.14	0.11	0.07	0.03	0.02	0.03	0.09	0.13	0.18
$\tau_x$ (month) $\mu_x$ (month/km) $\sigma_x$ (month/km) Females ( $x=1$ )   0.87   0.55   2.97 Males ( $x=2$ )   1.74   0.47   2.73												
Growth												
	$L_r$ (mm)	$t$ (month <sup>-1</sup> )	$t_0$ (month)	$\alpha$	$\phi$							
Females ( $x=1$ )	42	0.27	0	0.002 6	2.67							
Males ( $x=2$ )	37	0.17	0	0.002 4	2.72							
Values												
L (mm)												
	<9	9-19	19-24	24-26	25-36	>36						
$v_L$ (\$)	0	1.7	5	7	9.7	15.2						
Reproduction												
Month ( <i>i</i> )												
	1	2	3	4	5	6	7	8	9	10	11	12
$\zeta_i$	0.8	0.7	0.57	0.46	0.4	0.4	0.46	0.57	0.7	0.8	0.86	0.86
$a = 14.7$ $b = 0.46$ $h = 5 \times 10^6$ $m = 2 \times 10^6$												

of each month. Weight  $W_{i,j,x}$  is an allometric function of length  $L_{i,j,x}$  with parameters  $\alpha$  and  $\phi$  and therefore monthly yield is given by

$$Y_{i,j,x} = C_{i,j,x} W_{i,j,x} \quad (13)$$

Value (revenue per animal)  $v_L$  is a function of commercial-size categories  $L$ . Given values of  $v_L$  and the growth function a matrix of month, cohort and sex dependent values  $v_{i,j,x}$  can be computed. Thus, value of the catch  $V_{i,j,x}$  was modelled as,

$$V_{i,j,x} = C_{i,j,x} v_{i,j,x} \quad (14)$$

The simulation also computes egg production,  $E_{i,j}$ , with the relationship:

$$E_{i,j} = P_{i,j} \bar{N}_{i,j,1,s} Q_{i,j} \quad (15)$$

where

$$P_{i,j} = \frac{\zeta_i}{1 + e^{a - bL_{i,j,1}}} \quad (16)$$

is the proportion of mature females (Restrepo and Watson, 1991) and,

$$Q_{i,j} = h + m L_{i,j,1} \quad (17)$$

is the average fecundity of individual females.

Equilibrium values of yield-per-recruit  $Y/R$ , value-per-recruit  $V/R$ , and egg-per-recruit  $E/R$  are computed by summing the variable of interest for all cohorts throughout their lifetimes and dividing it by

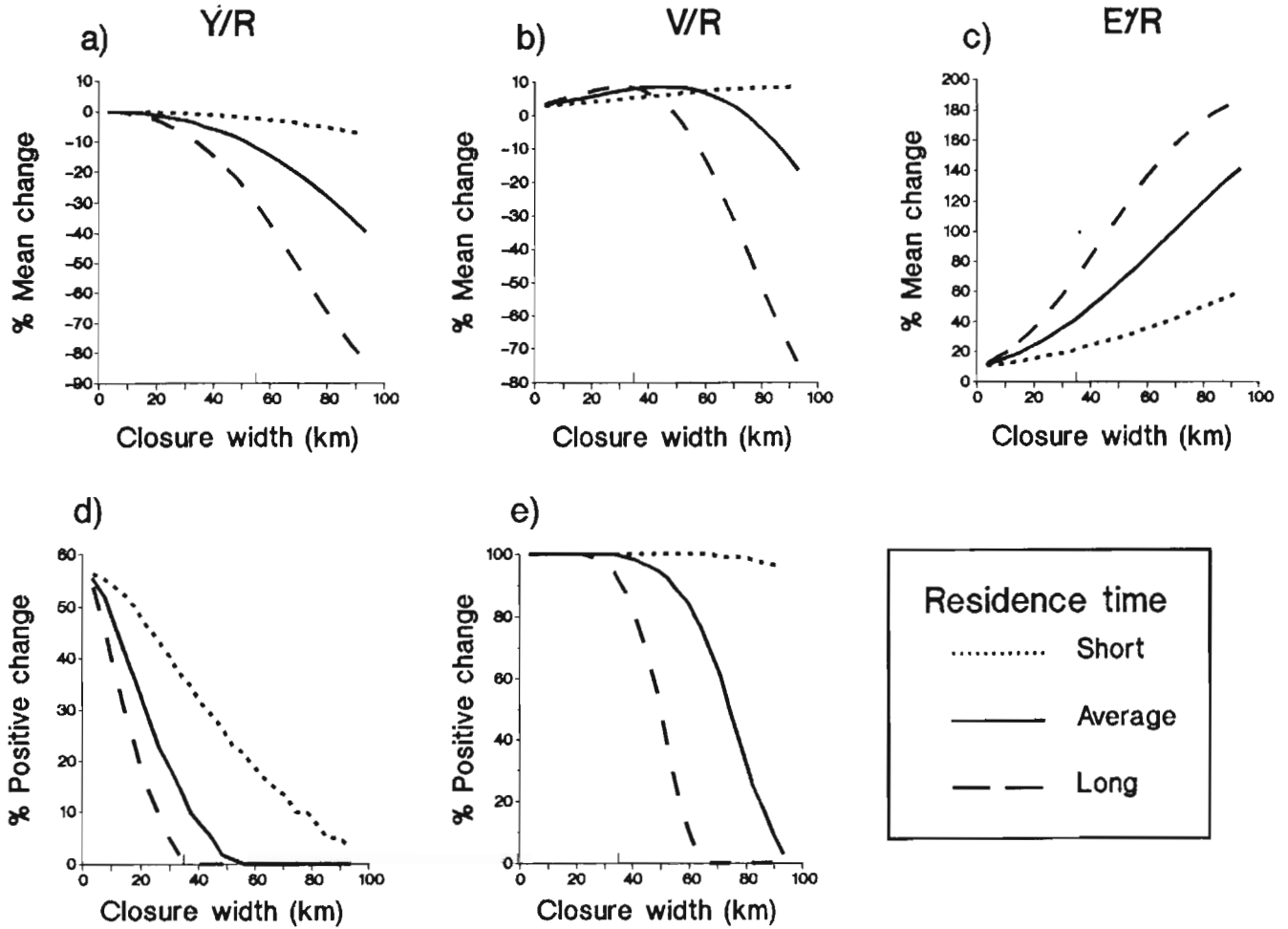


Figure 1. — Percent mean change in (a) yield-per-recruit, (b) value-per-recruit, and (c) egg-per-recruit; % positive mean change in (d) yield-per-recruit and (e) value-per-recruit for three residence times: long (150% of  $\beta_x$ ), average ( $\beta_x$ ), and short (50% of  $\beta_x$ ).

the number of recruits,

$$Y/R = \sum_{i=1}^{12} \sum_{j=1}^{12} \sum_{x=1}^2 Y_{i,j,x} / \sum_{i=1}^{12} \sum_{x=1}^2 N_{i,i,x,1}, \quad (18)$$

$$V/R = \sum_{i=1}^{12} \sum_{j=1}^{12} \sum_{x=1}^2 V_{i,j,x} / \sum_{i=1}^{12} \sum_{x=1}^2 N_{i,i,x,1}, \quad (19)$$

$$E/R = \sum_{i=1}^{12} \sum_{j=1}^{12} E_{i,j} / \sum_{i=1}^{12} \sum_{x=1}^2 N_{i,i,x,1} \quad (20)$$

**Case study: Torres Strait tiger prawn fishery**

To illustrate this model we used parameters which approximate those of the trawl fishery for the penaeid shrimp, *Penaeus esculentus* (Haswell, 1979, known as tiger prawn), in Torres Strait, far northern Australia (table 2).

Relative monthly recruitment values were taken from Blyth *et al.* (1990), and the seasonal pattern of relative fishing mortality of fully selected shrimp was obtained from commercial logbook data (Watson *et al.*, 1990 b). Data on movement of tagged tiger prawns (Watson unpublished data) were used to estimate residence times and their associated variances. Monthly proportions of mature females were obtained from Restrepo and Watson (1991), and fecundity estimates from Crocos (1987). Estimates of natural mortality, the growth function, the length-weight relationship and the vector of size-specific values (revenue per animal) were obtained from Watson and Restrepo (in press).

Although all other parameters were assumed to be known without error, fishing and natural mortality rates are unknown, and only empirically derived ranges were available. In order to incorporate the uncertainty associated with mortality estimates, the simulations were carried out with a large number of combinations of mortality values. Values of mortality were

obtained by scaling the estimates of the instantaneous coefficients of natural and fishing mortality with multiplicative factors ( $F_{\text{mult}}$  and  $M_{\text{mult}}$ ) as in Watson *et al.* (in press). To investigate the sensitivity of the results to the value of residence time  $\beta_x$ , simulations were run for three different values of this parameter. These values represent an average residence time (the best estimate of  $\beta_x$ , from tagging), a long residence time (150% of the best estimate of  $\beta_x$ ), and a short residence time (50% of the best estimate of  $\beta_x$ ).

Simulations were run for all mortality combinations and a range of closure widths, including a baseline run for no closure (width=0). Results presented correspond to percent change in per-recruit values with respect to those from the baseline run, and a given combination of fishing and natural mortalities. In addition, the proportion of combinations giving a positive change in per-recruit values from the baseline run were computed. For one closure, (35 km wide) we present the frequency distribution of per-recruit values, in order to examine the uncertainty associated with the evaluation of a particular spatial closure strategy.

## RESULTS

### Yield-per-recruit

Mean change in yield-per-recruit for all closure widths was negative and declined fastest for the long residence time (*fig. 1a*). Mean change in yield-per-recruit differed between residence times by less than 10% for closures less than 35 km wide. The percentage of simulations which predicted a positive change in yield-per-recruit (% positive change) was less than 55% for all three residence time (*fig. 1d*). These percentages decreased very rapidly as a function of closure width and reached a value of zero for widths of 35, 55 and 95 km and for the short average and long residence times respectively.

### Value-per-recruit

Mean change in value-per-recruit increased monotonically for the short residence time as a function of closure width (*fig. 1b*). For the other two residence times mean change in value-per-recruit increased to a maximum and then decreased rapidly. A maximum mean change in value-per-recruit of 7% was reached for a closure width of 35 km and a long residence time. For the average residence time a 9% maximum mean change in value-per-recruit is reached for a closure width of 45 km. The frequency of positive changes in value-per-recruit remains around 100% for closures of less than 25, 35 and 85 km, and for long, average and short residence times respectively (*fig. 1e*). The frequency of percent positive drops very rapidly as closure width increases and reaches

zero for closure widths of 60 and 95 km for long and average residence times respectively. For the short residence time, the frequency of positive changes does not drop significantly for the range of closure widths examined.

### Eggs-per-recruit

Irrespective of the residence time, all closures resulted in a positive mean change in egg-per-recruit (*fig. 1c*). In fact, all parameter combinations resulted in increases in egg-per-recruit, that is the frequency of positive changes was always equal to 100%. Mean change in egg-per-recruit increased monotonically with closure width. The highest increases in mean egg-per-recruit were 50, 130 and 180% for short, average and long residence times, respectively. Closure widths which produced mean change in egg-per-recruit of 50% were 90, 45 and 30 km for short, average and long residence times, respectively.

### 35 km closure

Mean change in yield-per-recruit for a 35 km closure ranged from -1 to -8% as a function of residence time (*fig. 1a*). For the same closure width from 0 to 38% of simulations resulted in increases in yield-per-recruit (*fig. 1d*). The frequency distribution of percent change in yield-per-recruit revealed that positive or negative changes in yield larger than 10% are possible (*fig. 2a*). Mean change in value-per-recruit for this closure ranged from 4% to 6% (*fig. 1b*). Increases in value-per-recruit were observed in 95% to 100% of simulations (*fig. 1e*). The frequency distribution of percent change in value-per-recruit showed increases of up to 30% (*fig. 2b*). For the 35 km closure width a 20 to 80% mean increase in mean egg-per-recruit was observed (*fig. 1c*). Predicted change in egg-per-recruit significantly varied with residence time, ranging from no increase to increases of over 100% (*fig. 2c*).

## DISCUSSION

Spatial closure benefits have to be weighed against the costs associated with their establishment and maintenance. Enforcement is generally harder for a spatial closure than a temporal one, specially in remote areas, and non-compliance with the regulation can significantly erode their benefits (Die and Watson, in press). In some cases a combination of spatial and seasonal closures may best isolate under-sized animals and offer a better management strategy (Courtney *et al.*, 1991). Nevertheless, spatial closures may also be good substitute for size regulations, and avoid problems with excessive discarding of smaller animals (Nance *et al.*, 1989). They can also offer

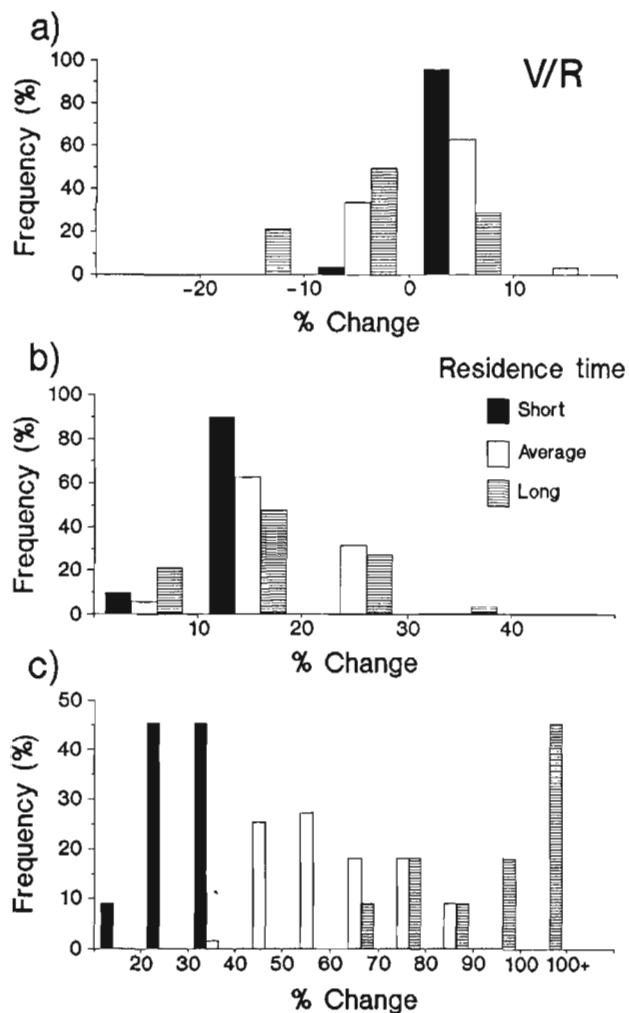


Figure 2. — Distribution of change for a 35 km closure for (a) yield-per-recruit, (b) value-per-recruit and (c) egg-per-recruit for three residence times: long (150% of  $\beta_x$ ), average ( $\beta_x$ ), and short (50% of  $\beta_x$ ).

protection to certain habitats such as inshore seagrasses which are essential for many tropical penaeid fisheries (Coles and Lee Long, 1985), and for the juveniles of many commercially important fish.

Different methods have been used to assess the potential benefits of spatial closure regulations. Nichols (1983) used Y/R analysis, simulation modelling, and comparisons of catch per unit of effort to evaluate Gulf of Mexico shrimp closures. Grey and Buckworth (1983) used size composition data to evaluate closures in the Gulf of Carpentaria shrimp fishery. Our study presents another alternative method with the simplicity of utility-per-recruit analysis but which also allows for the incorporation of some parameter uncertainty and extra details on biological and fishery dynamics.

Our model assumes there is a single direction of migration, from the inshore (closed) to the offshore

(open) area. Thus all that is required to model movement are net migration rates, obtainable from tagging studies. Obviously, the greater the spatial size-stratification, the more likely a spatial closure can be used to protect certain size groups.

Fishing is assumed to be randomly distributed within the open area, which may not always reflect observations of fleets concentrating in the vicinity of the closure boundary. In such cases a model with a greater spatial resolution may be required. Our model also assumes that animals are available to fishing throughout their entire life history. Nevertheless if necessary, it would be easy to incorporate further complexity such as a constraint on the largest size shrimp harvested, or other areas outside the closure where fishing may not occur, into a similar model.

The assumption that the effect of a spatial closure on the seasonal pattern of effort can be modelled by lagging such pattern by the residence time (equation 9) may be overly simplistic. Changes in biomass within the open area are unlikely to be linearly related to residence time, therefore it is possible the seasonal fishing pattern may be altered differently than what we propose. For instance the observed variability in migration speed suggests that the seasonal changes in biomass would be weaker offshore than inshore. Therefore a fishery in offshore waters may be less seasonal than an inshore fishery. Such detailed modelling of the dynamics of biomass and effort were outside the scope of this paper. Further research would be required to evaluate the effects on yield-per-recruit and/or value-per-recruit of such changes in the fishing pattern.

In our model the size and age of recruits entering the closed area is constant. Observations from surveys (Blyth *et al.*, 1990) suggest that there may be recruitment to the fishing grounds of larger animals at certain times, and that this pattern may vary from year to year. If these "large recruits" are targeted by the inshore fishery, a spatial closure may prevent their capture by the fleet, hence reducing closure benefits. Further research is required to develop a model which can accommodate such a scenario.

In this study maturation and fecundity were assumed to be related directly to size (or age). If the spatial distribution of spawners and their fecundity is not solely the result of size-stratification, then the model may not properly evaluate the effects of closures on egg-per-recruit. This spatial stratification related to reproductive development is common in fish stocks where there are several age groups of reproductively active adults. Penaeid shrimp, however, only live one or two years, and are unlikely to have such spatial segregation of the adult components of the stock. In some shrimp stocks migration and growth rates may vary between cohorts. While this could easily be incorporated in our model, such differences will very likely reduce spatial size-stratification and reduce the benefits of spatial closures.

Our value-per-recruit analysis does not incorporate fishing or enforcement costs. It is likely that these costs increase with distance offshore, therefore eroding the benefits of large spatial closures. If animals disperse whilst migrating offshore, catchability may also decrease as a function of closure width. This would further diminish the advantages of such a regulation.

The lack of complete biological data has been cited as a reason for not attempting to quantify the effects of a spatial closure (Grey and Buckworth, 1983). We have shown here, like other authors before [Watson and Restrepo, in press; Watson *et al.*, in press (a); Die and Watson in press], that parameter uncertainty can be incorporated successfully in the modelling process providing results which are useful to fisheries managers. Such results contain not only information on the most likely effect of the closure but also some indication on the uncertainty associated with the predictions.

For the Torres Strait shrimp fishery, and within the limits of the model, we have shown that spatial closures can be used to improve value-per-recruit and egg-per-recruit. Other authors report similar effects of spatial closures (Nance *et al.*, 1989; Nichols, 1983). For the tiger prawn fishery in Torres Strait, establishment of closures of less than 35 km width would have little chance of large losses in yield-per-recruit while likely increasing value-per-recruit and egg-per-recruit. Closures wider than 35 km, however, would certainly lead to significant losses in yield-per-recruit and increase the likelihood of reductions in value-per-recruit. Such negative effects would have to be weighed against the potential benefits to egg-per-recruit. Fishery managers tend to be risk-averse in relation to decisions about changes in yield-per-recruit or value-per-recruit. They may find difficult to decide between trading losses in yield-per-recruit and value-per-recruit against increases in egg-per-recruit, specially

in the absence of information about the stock-recruitment relationship.

Substantial work on spatial and seasonal closures for penaeid fisheries has been carried out in the Gulf of Mexico. Watson *et al.* [in press (a)] highlighted some of the differences between the management of these North American fisheries, and those from Northern Australia. In the Gulf of Mexico for instance, inshore spatial closures had the effect of allocating resources away from the "bay fleet" and towards the offshore fleet. Such redistribution of the resource created conflicts between the two user groups.

In Northern Australia the remoteness of the fishing grounds has led to a more homogeneous fleet than the one in North America. Therefore it is less likely that spatial closures in Northern Australia lead to conflict between inshore and offshore fleets. The Northern Australian fisheries however, are limited entry and grouped in different management units (Gulf of Carpentaria, Torres Strait, Queensland east coast). A given boat can have a fishing license for one or more of these units. Because spatial closures, like seasonal closures, prevent fishers to access parts of the resource, it is to be expected that some interaction between management units can occur. In fact the experience in Northern Australia is that fishing closures in general, are often proposed by the local fleet to exclude outside boats. Such tendency highlights the problems of resource allocation that closures may produce.

We have shown that with the approach outlined here, spatial closures may be beneficial to a specific fishery such as the Torres Strait tiger prawn fishery. The magnitude of these benefits are comparable to those demonstrated by Watson *et al.* [in press (a)] for seasonal closures. There are, however, a number of unresolved issues, such as spatial closure effects on mixed-species fisheries, the effects of combinations of seasonal and spatial closures, which should be addressed in future modelling studies.

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