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# Bioeconomic modelling and risk assessment of tiger prawn (Penaeus esculentus) stock enhancement in Exmouth Gulf, Australia

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#### **Abstract**

A bioeconomic model was developed to evaluate the potential performance of brown tiger prawn stock enhancement in Exmouth Gulf, Australia. This paper presents the framework for the bioeconomic model and risk assessment for all components of a stock enhancement operation, i.e. hatchery, grow-out, releasing, population dynamics, fishery, and monitoring, for a commercial scale enhancement of about 100 metric tonnes, a 25% increase in average annual catch in Exmouth Gulf. The model incorporates uncertainty in estimates of parameters by using a distribution for the parameter over a certain range, based on experiments, published data, or similar studies. Monte Carlo simulation was then used to quantify the effects of these uncertainties on the model-output and on the economic potential of a particular production target. The model incorporates density-dependent effects in the nursery grounds of brown tiger prawns. The results predict that a release of 21 million 1 g prawns would produce an estimated enhanced prawn catch of about 100 t. This scale of enhancement has a 66.5% chance of making a profit. The largest contributor to the overall uncertainty of the enhanced prawn catch was the post-release mortality, followed by the densitydependent mortality caused by released prawns. These two mortality rates are most difficult to estimate in practice and are much under-researched in stock enhancement.

Keywords: Bioeconomic modelling; Risk assessment; Stock enhancement; Tiger prawn; Penaeus esculentus

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#### 1. Introduction

The world's fishery resources are under threat from habitat degradation and over exploitation (Brown and Day, 2002). In addition to the regulations of fishing for sustainable fisheries, stock enhancement represents

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a potential component of an economically viable and ecologically sound management strategy to replace extinct stocks for recreational or commercial fishing, to rebuild depleted stocks, and to augment existing but perhaps overexploited stocks (Hilborn, 1998; Travis et al., 1998; Leber, 2002). Enhancing depleted stocks by stocking is appealing because of its straightforward logic – releasing large numbers of artificially raised juveniles into the marine environment is assumed to compensate for the enormous natural mortality in the early stages of the life cycle or the low production of juveniles due to overfished spawning stocks and thereby increase the stock size and fishery production (Travis et al., 1998). Its outcome, however, is difficult to predict because it involves many unknowns and complex issues such as interactions between the released and wild animals, unknown effects on population dynamics including density-dependent effects, ecosystem processes, and resource economics. A stock enhancement project usually demands a large sum of capital investment, continuing investment for the production and release of juveniles and monitoring and assessment of its success by management. Before initiating any such large, complex project, a thorough risk assessment can certainly assist in making the right decision, or identifying potential problems for stock enhancement, and thus prevent wasting resources.

Stock enhancement is not a fully experimental discipline (Leber, 2002). Evaluating its performance and assessing its risk through a real experiment is very costly and almost impossible in most instances. Mathematical modelling, however, provides an economical and powerful tool for simulating and predicting the likely outcomes of the system that has many different components changing simultaneously. Its advantages and feasibility have long been recognized, and modelling has been recommended as an essential part of any enhancement project (Blankenship and Leber, 1995; Rothlisberg et al., 1999). This study developed

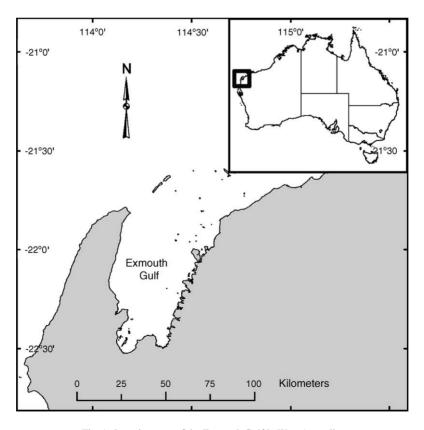


Fig. 1. Location map of the Exmouth Gulf in West Australia.

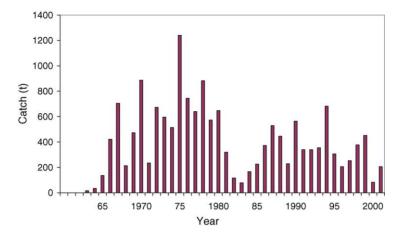


Fig. 2. Annual landings of the tiger prawn fishery in Exmouth Gulf, Australia.

a comprehensive model for the bioeconomic analysis of tiger prawn stock enhancement in Exmouth Gulf.

All the components of stock enhancement are subject to uncertainty from either environmental variations or technical deviations. To incorporate this uncertainty in predicting the performance from an enhancement, we used Monte Carlo simulation instead of deterministic modelling. Model parameters were not supposed to take single point values, but to assume a distribution over a certain range, which was derived from experiments, other similar studies, or expert judgements. The various parameters were assumed to vary independently because of a lack of information about the correlations between parameters. Combinations of parameter values that produced improbable results were not considered. With Monte Carlo simulation, we can quantify the effects of these uncertainties on model-output results and then carry out risk analysis for some management targets or evaluate the probability for certain outcomes of interest to the industry.

The brown tiger prawn (*Penaeus esculentus*) in Exmouth Gulf has a short life cycle of about 1 year and grows fast (Penn and Caputi, 1986). It takes only 16 weeks from the release size of 1 g to the commercially fishable size of 20 g (Haywood et al., 1995). Exmouth Gulf is semi-closed, and the brown tiger prawns form a single unit stock within the Gulf (Fig. 1) (Penn and Caputi, 1985). The small area and the semi-closured nature of the Gulf provide a relatively calm environment which is believed to be beneficial to the survival

of released prawn juveniles and assure a high recapture rate if they survive till the fishing season.

The historical annual landings of the fishery show clear periods: a development to full exploitation period of high catches in the 1970s, followed by a sharp decline by the early 1980s, and a recovery-managed period of constrained landings after the mid-1980s (Fig. 2). Since the mid-1980s, the annual catch of P. esculentus fluctuated from 650 t in 1994 to 82 t in 2000, with an annual average catch of about 390 t. It is believed that the maximum sustainable production in Exmouth Gulf may lie around 600t, without considering the high levels exhibited in the 1970s. In discussions with researchers, industry and managers, an enhancement target of about 100 t was thought to be feasible without introducing large density-dependent effects because it is presumed that tiger prawn populations would still be well below the presumed carrying capacity of Exmouth Gulf following enhancement. This enhancement project was designed to augment the existing stock and dampen fluctuation in catch due to variable recruitment.

Experiments of hatching and growing juvenile *P. esculentus* in raceways were successfully carried out by CSIRO Marine research and MG Kailis Group in both Brisbane, Queensland and in Exmouth Gulf, Western Australia (Crocos et al., 2003). Data on biology and economics from these experiments, data from the Exmouth Gulf brown tiger prawn fishery and information from other studies relevant to *P. esculentus*, were used

to develop the bio-economic model which was then used to evaluate risks for the brown tiger prawn stock enhancement in Exmouth Gulf.

#### 2. Materials and methods

#### 2.1. The bioeconomic model

The bio-economic model consists of six components: hatchery, grow-out, transport, nursery, fishery, and monitoring (Fig. 3). The enhanced and wild prawns are treated separately as two sub-stocks in population dynamics, but density-dependent effects are assumed to occur in the nursery ground i.e. natural mortality for the wild stock arises due to the increased density caused by releasing captive-reared juveniles into the sea. The enhanced population covers from the spawning of brood stocks through to the end of fishing, and the wild population covers from the time from natural recruitment to the nursery grounds through to capture in the fishery. Weekly time steps were used in the model to capture the seasonal nature of tiger prawn growth.

# 2.1.1. Hatchery

The hatchery component comprises the brood stock and the hatched larvae. A detailed prawn hatchery model, containing the costs for using either wild or domesticated brood stock, has been developed by Preston et al. (1999). The bioeconomic model in this study uses Preston's et al. (1999) model for the hatchery component and contains only its outputs, the number of larvae produced, Q, and the cost per larva,  $\eta$ . Total cost from

hatchery is then,

$$\Omega_{\rm h} = \eta Q^{\varphi} \tag{1}$$

where  $\varphi$  is a parameter describing the economy of scale and normally assumes a value smaller than 1, meaning that the unit costs of production decline as the scale of production increases. The actual cost of producing a 15 day-old post-larva (PL15) for stocking in the raceways, based on the trials in Brisbane and Exmouth Gulf, was AUD\$0.018 per PL15.

# 2.1.2. Juvenile production

This part covers the time from stocking the raceways with PL15 to the release of the juvenile prawns in the nursery. In this component, the number of larvae is presumed to follow an exponential decay process. Given initial number of larvae,  $N_0$ , and natural mortality rate,  $M_t$ , the total number at week t is calculated as,

$$N_t = N_0 e^{-\sum_{i=1}^t M_i}$$
 (2)

In the early life stages, the mortality rate changes dramatically over time but this variation is believed to be related more to body size than time (Beyer et al., 1999). Most empirical studies show that the relationship between mortality and size is better described with a power model (Pepin, 1993; Lorenzen, 1996, 2000; Munch et al., 2003):

$$M_t = aL_t^{-b} (3)$$

where  $L_t$  is the carapace length at week t, a and b are parameters defining how mortality changes with size in the population. This relationship differs between the

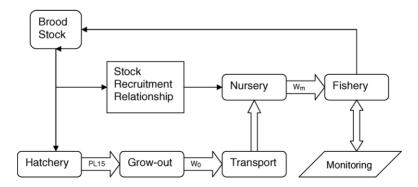


Fig. 3. Schematic representation of the bioeconomic model.

artificial grow-out and post-release periods, i.e. *a* and *b* assuming different values.

Individual growth in the early life stages is better modelled through weight because the commonly used von Bertalanffy equation is often inconsistent with the measured growth (Gulland, 1983). An exponential function is assumed here,

$$W_{t+1} = W_t e^{\delta_t} \tag{4}$$

where t is the age in weeks, and  $\delta_t$  is the growth rate at week t. To accommodate for the fast change in growth rate from post-larvae to juveniles,  $\delta_t$  assumes a different value each week, based on experimental results, up to the release size. The length–weight relationship is supposed as,

$$W_t = cL_t^d \tag{5}$$

The number of raceways required, y, is a function of the area of each raceway, A (m<sup>2</sup>), the maximum biomass density at which prawns can be held,  $\rho_{\rm max}$  (kg m<sup>-2</sup>), and the total biomass of juvenile prawns,  $W_{\rm max}$  (kg), to be held,

$$y = \frac{W_{\text{max}}}{\rho_{\text{max}} A} \tag{6}$$

The production cost includes the capital investment for hardware facilities and the operating costs. The capital cost consists of two components, alternative cost and the cost of real depreciation and maintenance (Hannesson, 1993). The former is normally calculated based on a discount rate, which reflects the alternative rate of return on investment, and the latter is computed through a depreciation rate, which is the inverse of the lifetime of the equipment in question. However, due to the special circumstances of the fishery, the capital cost was excluded from the model. The operating cost consists of expenditures on prawn feed, salary and pumping. The total production cost of juveniles can be calculated,

$$\Omega_{g} = y(A\sigma + \psi) + (B_{e} - B_{i})\gamma\tau \tag{7}$$

where  $\sigma$  is the weekly cost of pumping per m<sup>2</sup> of raceway,  $\psi$  is the salary costs of maintaining one raceway,  $B_{\rm i}$  and  $B_{\rm e}$  are the initial and end total biomasses of all grow-out juveniles,  $\gamma$  is the cost of feed per kg, and  $\tau$  is the conversion ratio of food to growth in biomass. Our experiments show an average survival rate of 67.5%

from PL15 to 1 g size at release and that producing one million 1 g *P. esculentus* in raceways would require 1.5 million PL15s with the estimated operating costs of AUD\$27,000. The linear cost function (Eq. (7)) is simplification of a real grow-out system. However, no experimental data has been available so far to allow for the expression of economy of scale. The cost function could be refined when more experimental enhancements have been completed.

## 2.1.3. Transport

The number of prawn juveniles, n, carried per tanker/vessel is estimated as.

$$n = \frac{V}{W_t \theta} \tag{8}$$

where V is the volume of the tanker/vessel,  $W_t$  is the weight of each prawn at the time of transport and  $\theta$  is the seawater volume desired for unit biomass during the transport. The number of trips of the tanker/vessel are therefore  $N_t/n$ , where  $N_t$  is the number of juvenile prawns produced in the production and to be released in the nursery area. The harvest and transport from raceways to release sites may cause the death of some juveniles. This mortality is incorporated into the model by multiplying the number of juveniles out of the raceways with a single survival rate,  $\phi$ . The number of days, D, required to release all prawns is,

$$D = \frac{\phi N_t}{nT_{\rm r}} \tag{9}$$

where  $T_r$  is the number of trips per day that can be made. Transport costs are therefore the product of the number of days and the operating costs of each day  $T_c$ .

$$\Omega_{\rm T} = T_{\rm c}D\tag{10}$$

### 2.1.4. Nursery ground

There are two sub-components in the model description of the nursery ground, one corresponding to the wild stock and one to the enhanced stock. They have the same structure and only differ in the timing and the number of prawns entering the nursery. The enhanced stock sub-component includes juvenile prawns from the time they are released to the time they recruit to the fishery. The size of released prawns can range from the size of a larva, to that of a recruit. The wild stock

Table 1 Parameters and their values/distributions in the bioeconomic model

Parameter and stage of enhancement	Description	Value/distribution	Equation
Hatchery			
η (\$/PL15)	Cost per larva	T(0.01,0.018,0.02)	1
Q (PL15)	Number of larvae	$31.5 \times 10^6$	1
Grow-out			
a	Parameter defining mortality-length relationship	N(0.127, 0.1)	3
b	Parameter defining mortality-length relationship	<i>N</i> (-0.99,0.1)	3
$\delta_1$	Growth rate	1.92,1.01,0.66,0.49,0.39,0.36,- 0.34,0.33,0.30	4
$A (m^2)$	Area of a raceway	50	6
$\rho_{\rm max}~({\rm kg/m^2})$	Maximum biomass density	T(2,3,3.5)	6
$\sigma$ (\$/week m <sup>2</sup> )	Cost of water pumping	2.422	7
τ	Conversion ratio of food to growth	T(1.15,1.3,1.4)	7
γ (\$/kg)	Cost of feed	4.75	7
$\psi$ (\$/raceway)	Maintenance cost of one raceway	139.4	7
$W_0$ (kg)	Individual juvenile weight	0.001	
Transport			
$\theta$ (seawater/biomass)	Sea water volume for unit biomass	U(10,20)	8
$V(m^3)$	Volume of a tanker	1.0	8
$T_{\rm r}$ (trips/day)	Number of trips a day	1	9
$T_{\rm c}$ (\$/trip)	Trip cost	750	10
$\phi$ (%)	Mortality rate	U(1,5)	
Nursery			
$L_{\rm m}$ (mm)	Maximum length	16.0	
$W_{\rm m}$ (kg)	Maximum weight	0.006	
a	Parameter defining mortality—length relationship	N(1.05,0.2)	11 (3) <sup>a</sup>
b	Parameter defining mortality-length relationship	-1.00	11 (3)
$M_{\lambda}$	Density-dependent mortality rate	ln(-3.15,0.55)	A3
$M_{1,\lambda}$	Density-dependent mortality rate for enhanced prawns	$0.5M_{\lambda}$	11
$M_{2,\lambda}$	Density-dependent mortality rate for wild prawns	$0.5M_{\lambda}$	11
$W_0$ (kg) (wild)	Individual juvenile weight	0.001	
δ	Weight growth rate	0.9 (wild) 0.82 (released)	12
$\kappa_t$	Seasonal growth factor	Fig. 4	12
Fishery			
M (1/week)	Natural mortality rate	N(0.045,0.02)	13
q (1/week.effort)	Catchability coefficient	0.001	14
$L_0$ (mm)	Length of zero retention	25	15
$L_{100} \text{ (mm)}$	Length of 100% retention	30	15

Table 1 (Continued)

Growth parameters		Female	Male	
$\overline{L_{\infty}}$	Maximum length	N(40,2)	N(33,1.6)	16
k	Growth coefficient	N(0.05,0.01)	N(0.06,0.01)	16
c	Parameter defining	$3.73 \times 10^{-3}$	$2.07 \times 10^{-3}$	18 (16, 4)
	weight-length relationship			
d	Parameter defining	2.547	2.764	18 (16, 4)
	weight-length relationship			
$f(\mathbf{W})$	Relative price	Fig. 5		20
$p_{\text{max}}$ (\$/kg)	Price of largest grade of prawns	<i>U</i> (15,25)		21
$T_{\rm f}$ (week)	Week fishing season starts	14		21, 24
T (week)	Week fishing season ends	35		21, 24
I+I' (\$/boat-week)	Weekly cost of a fishing boat	10500		21
$\eta_{\rm m}$ (\$)	Monitoring cost at sea	7500		23
π	Genetic screaming cost	40		23
ω	Percent cost	15		24
α	Parameter defining	N(85.3,13.16)		A1
	stock-recruitment relationship			
β	Parameter defining	N(0.0468,0.0137)		A1
	stock-recruitment relationship			

T(a, b, c) means a triangular distribution with a minimum value of a, a maximum value of c, and the most likely value of b. N(a, b) indicates a normal distribution with a mean of a and a standard deviation of b. U(a, b) describes a uniform distribution between a and b.  $\ln(a, b)$  is a lognormal distribution with a log-mean of a and log-standard deviation of b.

sub-component includes prawns from larvae to recruits to the fishery. Survival and growth are size dependent. Growth varies seasonally, and survival is dependent on the prawn density (wild and enhanced) in the nursery. The timing and number of larvae settling in the nursery may vary. The abundance of the enhanced and wild stock in week *t* are modelled as.

$$N_{i,t+1} = N_{i,t} e^{-(M_{i,t} + M_{i,\lambda})}$$
(11)

where i=1 indicates enhanced and i=2 wild,  $M_{i,t}$  is the natural mortality that is calculated as a function of length using Eq. (3), but with different values for a and b (Table 1),  $M_{i,\lambda} = f(N_i)$  denoting the mortality rates that result from the increased density caused by releasing captive-reared juveniles into the sea. The calculation of the density-dependent mortality is detailed in Appendix A. The initial number of wild juveniles,  $N_{2,0}$ , in the nursery is a variable that is determined so that the mean catch from the wild stock is about 400 t, i.e. the long-term average catch observed over the last 35 years (Fig. 2).

Growth is still modelled in weight using an exponential function of parameter  $\delta$ , but modified by a factor,  $\kappa_t$ , to consider the seasonal difference in growth, which is equal to 1 at the peak of the growing season and is

smaller than 1 in the rest of the season,

$$W_{i,t+1} = W_{i,t}(1 + \kappa_t(e^{\delta_i} - 1))$$
 (12)

The average individual weight of enhanced juveniles  $W_{1,t}$  and wild juveniles  $W_{2,t}$  in the nursery area at any particular time t will not necessarily be the same. These weights depend on the week when the wild stock recruits to the nursery area, on the individual weight of enhanced juveniles released in such areas and on the week when these enhanced juveniles are released. Wild juveniles recruit to the nursery area during week  $J_0$  at weight  $W_0$ , the same weight that larvae for enhancement have when they start in the production.

The timing assumed for sub adult prawns to migrate out of the nursery is mainly related to size (O'Brien, 1994). Migration is modelled to occur at the same fixed size  $L_{\rm m}$  for both the enhanced and the wild prawns. The weight at migration is calculated by substituting  $L_{\rm m}$  in Eq. (5).

## 2.1.5. *Fishery*

The fishery consists of two components, one corresponding to the wild stock, and one to the enhanced stock. The model structure of these two components is exactly the same – they have been split to follow

<sup>&</sup>lt;sup>a</sup> The parameter is incorporated into Eq. (11) via Eq. (3).

changes in numbers of prawns from the wild and enhanced stocks separately. Each component has separate male and female populations. It includes prawns from recruits to adults (up to 1 year old). Growth is size, sex, and season dependent. Natural mortality is assumed to be constant during the fishing season. Fishing selectivity is size dependent, and fishing mortality of a certain size of prawn changes as a function of fishing effort. As differentiation in size and growth between sexes becomes clear at this stage, a subscript, j, is used to indicate different sexes in the equations hereafter, j = 1 for females and j = 2 for males.

Abundance in week t for stock i and sex j is modelled as,

$$N_{i,j,t+1} = N_{i,j,t} e^{-(M+F_{i,j,t})}$$
(13)

where  $F_{i,j,t}$  is the fishing mortality rate in week t for stock i and sex j calculated as,

$$F_{i,i,t} = qf_t S_{i,i,t} \tag{14}$$

where q is the catchability coefficient, f is the weekly fishing effort and S is the selectivity factor as,

$$\begin{cases}
S_{i,j,t} = 0 & L_{i,j,t} \le L_0 \\
S_{i,j,t} = \frac{L_{i,j,t} - L_0}{L_{100} - L_0} & L_0 < L_{i,j,t} < L_{100} \\
S_{i,j,t} = 1 & L_{i,j,t} \ge L_{100}
\end{cases}$$
(15)

where  $L_0$  is the largest length where the probability of retention is zero and  $L_{100}$  is the smallest length where probability of retention is 1. The mean length of the population is modelled with the Von Bertalanffy equation,

$$L_{i,j,t} = L_{\infty i,j} (1 - e^{-k_{i,j}t})$$
(16)

where  $L_{\infty}$  is the maximum length, and k describes the rate at which it approaches the limiting size. The stochasticity in growth is described by the distributions of  $L_{\infty}$  and k. As this study concentrates on the overall population, differences in growth between individual prawns were not modelled. Also note that the natural and fishing mortality rates of the enhanced and wild stocks in the fishery are assumed to be the same for prawns with the same carapace length.

The weekly prawn catch in week t are estimated from the normal fishing equation:

$$C_{i,j,t} = (N_{i,j,t} - N_{i,j,t+1}) \frac{F_{i,j,t}}{F_{i,j,t} + M}$$
(17)

The yields (catch in weight) are estimated as the product of the numbers caught and prawn weight,

$$Y_{i,i,t} = C_{i,i,t} W_{i,i,t} \tag{18}$$

where  $W_t$  is the weight of individual prawn in the middle of week t calculated via Eqs. (16) and (5). It is impossible to distinguish between enhanced and wild prawns. We, therefore, have assumed that they fetch the same market price. The value of the enhanced catch,  $V_{1,t}$ , and that of the wild catch,  $V_{2,t}$ , are then defined as follows.

$$V_{i,t} = \sum_{j} Y_{i,j,t} p_{j,t}$$
 (19)

where  $p_{j,t}$  is the price per kg catch and dependent on prawn size,

$$p_{i,t} = p_{\text{max}} f(W_{i,i,t}) \tag{20}$$

where  $p_{\text{max}}$  is the price per kg for the largest prawns and f(W) is the relative price defined in Fig. 5.

There are two categories of costs in fishing, fixed costs from long-term investment and variable costs from daily fishing operation of a boat. If the fixed cost per boat-week is  $I_t$ , and the variable expenditure for a boat-week fishing is  $I_t'$ , and the total cost of fishing over a season is.

$$\Omega_{\rm f} = \sum_{t=T_{\rm f}}^{T} (I_t + I_t') \tag{21}$$

where  $T_f$  and T are the starting and end weeks of the fishing season, which were 10th April and 13th November in Exmouth Gulf.

# 2.1.6. Monitoring

Stock enhancement may introduce diseases, affect the genetic diversity of the stock and have other consequences for the wild stock due to density-dependent effects. These potential risks should be carefully monitored. We have designed and incorporated a monitoring plan into the model. With this sub-model, we can estimate the sample requirements to effectively estimate the proportion of released prawns in the total population with a certain statistical power and the minimum sample size required to achieve a minimum number of recaptures of enhanced prawns. The appropriate distribution for this experiment is the binomial (Hilborn and

Walters, 1992). The probability of obtaining at least z enhanced prawns in a sample of m prawns randomly sampled from the commercial catch is,

$$p(z) = 1 - \sum_{v_i=1}^{z} p(v_i; m, \theta)$$
 (22)

where  $p(x; m, \theta)$  is a binomial distribution function, and  $\theta$  is the proportion of enhanced prawns found in the catch.

The costs of monitoring considered here are the cost of obtaining m adult prawns at sea,  $\eta_m$ , for genetic screening and the cost of genetic analysis for each prawn,  $\pi$ . Total monitoring costs are therefore calculated as.

$$\Omega_{\rm m} = \eta_{\rm m} + m\pi \tag{23}$$

No costs of fishing the "extra" enhanced stock were included in the model as we assumed that enhancement increases prawn abundance and no extra fishing effort is needed to catch the enhanced prawns. The Exmouth Gulf prawn fishery has a strict control over licenses and a fixed duration of fishing season. It is reasonable to assume that no increase in fishing effort would occur after stock enhancement. However, the on-vessel processing of the catch from the enhanced stock does incur costs because remuneration of crew members is partially paid as a percentage of catch value,  $\omega$ . After estimating all the revenues from prawn landings and costs for hatchery, grow-out, transport, fishing and monitoring, the revenue from the enhancement is then,

$$P_1 = (1 - \omega) \sum_{t=T_f}^{T} V_{1,t} - \Omega_h - \Omega_g - \Omega_T - \Omega_m \quad (24)$$

where  $\Omega_h$  is given by Eq. (1),  $\Omega_g$  by Eq. (7),  $\Omega_T$  by Eq. (10), and  $\Omega_m$  by Eq. (23), respectively. The profit from the wild fishery is

$$P_2 = \sum_{t=T_{\rm f}}^{T} V_{2,t} - \Omega_{\rm f} \tag{25}$$

# 2.2. Model parameters

The parameters for hatchery, grow-out, and transport were estimated from the data collected during the feasibility study and the first stage of the project (Loneragan et al., 2003) (Table 1). The parameters describing the relationship between mortality and length (Eq. (3)) during the grow-out (Table 1) were estimated based on the mortality rates and lengths in different time intervals. The size at release was set at 1.0 g for the baseline simulation. A preliminary experiment carried out by the M.G. Kailis Group in West Australia showed no mortality during harvest and transport from raceways to release sites (Crocos et al., 2003). For precautionary purposes, however, this mortality was set to a likeliest value of 3%, with a uniform distribution ranging from 1 to 5% (Table 1).

The size at migration from the nursery was selected as 16.0 mm CL and 6 g based on discussions during two project workshops and results from studies on juveniles of the same species, *P. esculentus*, in Moreton Bay (O'Brien, 1994), Eastern Australia, at a similar latitude to Exmouth Gulf. The timing of migration may also be affected by environmental factors like rainfall, which is not predictable. We assumed that the average length at migration reflects the average environmental conditions.

The relationship between weight and length was derived from observations from the wild fishery. The post-release mortality rate was also a function of length (Lorenzen, 2000; Munch et al., 2003) and the parameters, a and b, were estimated from the data presented in O'Brien (1994) (Appendix B; Table 1). The growth of prawn juveniles in the nursery is likely to change with time as temperature and food availability varies over time. To model this effect of time on growth, a coefficient,  $\kappa_t$ , reflecting the seasonal pattern of temperature and food availability (Fig. 4) was incorporated into the growth equation (Eq. (12)). The hypothetical seasonal pattern was not derived experimentally, but rather based on the expected impact of changes in temperature and food availability.

The mortality rate due to the increased density caused by the released prawns was estimated from the density-dependent effect observed in the stock recruitment relationship (Appendix A). We assumed that such a density-dependent mortality applies equally to both the enhanced and wild prawns and takes effect until prawns migrate out of the nursery grounds. This assumption implies that stock enhancement has negative impact on wild catch because of the density-dependent mortality incurred to the wild stock. This economic loss to the wild fishery was not accounted for in the calcu-

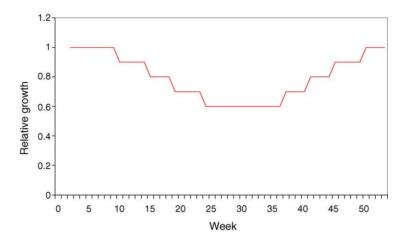


Fig. 4. The seasonal factor in growth (Eq. (12)), which is used to account for the fact that growth rate of prawns of same size changes with season, normally growing faster in summer than in winter.

lation of profit from stock enhancement. The density-dependent mechanism might change, however, depending on the relative sizes of enhanced and wild prawns. The natural mortality during the fishing season is assumed to have a constant value of 0.045 per week with a standard deviation of 0.02 per week following Watson et al. (1993) and Wang and Die (1996). The growth parameters for adult prawns are from White (1975). Gear selectivity,  $L_0$  and  $L_{100}$ , and catchability coefficient, q, were estimated based on the data from the brown tiger prawn fishery in Exmouth.

The fishing season for the tiger prawn fishery has been fixed at week 14 through to week 35. Daily cost for fishing was about AUD\$1500 per boat, and the cost to obtain prawn samples for genetic analysis was estimated at AUD\$7500, based on only salaries of scientists involved in fieldwork. The expense for genetically screening a single prawn was estimated at AUD\$40. Note that currently, the real costs of genetic analyses are not fully known because the technology for screening large numbers has not been developed and the feasibility of using micro-satellites for identifying enhanced

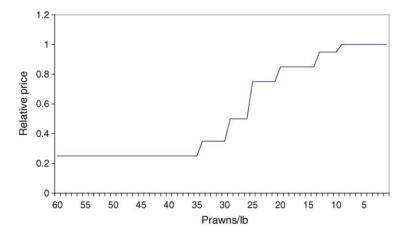


Fig. 5. Relative prices for prawns of different sizes, which multiplied by the maximum price,  $p_{\text{max}}$ , give absolute prices of prawns of different sizes (Eq. (20)).

prawns has not been fully developed (see Lehnert et al., 2003; Bravington and Ward, 2004; Loneragan et al., 2004). It should be noted that the monitoring component assumed that the enhanced prawns mix randomly with the wild prawns.

The price of prawns is a function of prawn size (Fig. 5). The maximum price was expected to have a uniform distribution between 15\$/kg and 25\$/kg based on the market prices observed over the last few years. As prawns in Australia are mainly exported to Japan and the USA, the additional 100 t of prawns produced by stock enhancement in Exmouth Gulf, would have no impact on the prawn price of the large international market.

Generally, few estimates of parameter uncertainty were available. Some parameters can be estimated well (e.g. length weight relationship, gear selectivity), and some others have limited impact on the uncertainty of the predictions (e.g. salary costs of production, size at emigration from the nursery), although their estimates do contain uncertainty. These two kinds of parameters were excluded from the uncertainty analysis. For other parameters, we examined the minimum and maximum values of the parameter reported from different sources or for different species (e.g. survival rates in the nursery, prawn prices) because some biological parameters show little variation within a species or even among similar species (Myers et al., 1999). For some other parameters, we made educated guesses about their minimum and maximum likely values (e.g.

transport mortality). Four types of probability distributions were used, normal, lognormal, uniform and triangular, depending on the reliability of the estimated values and our knowledge.

### 2.3. Sensitivity analysis

The bio-economic model consists of many parameters, each with a different influence on the predicted outputs of the model. Identifying the most influential parameter provides an efficient way of improving the results by fine-tuning the estimate of that parameter. A sensitivity analysis was carried out, therefore, to investigate how different variables affected the forecasts from the model. Sensitivity was calculated by computing the rank correlation coefficients between every assumption and every forecast while the simulation is running. The correlation coefficients provide a meaningful measure of the degree to which the assumptions and forecasts change together. Squaring the rank correlation coefficients and normalizing them to 100% gives the sensitivity as a percentage of the contribution to the variance of the target forecast.

#### 3. Results

Ten thousand simulations were carried out, and the model estimated that 21 million 1 g juveniles would need to be released into the sea to produce a median

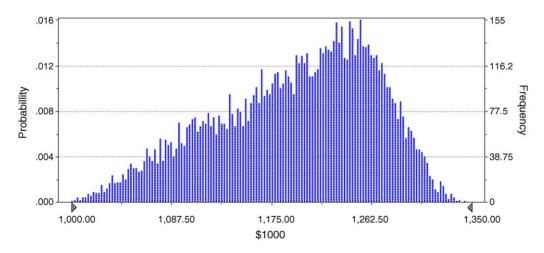


Fig. 6. Raceway production costs to produce 100 t of enhanced prawns.

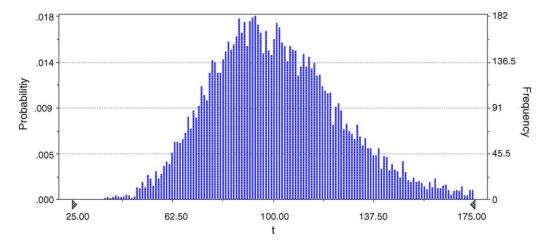


Fig. 7. Catch predictions for the enhanced stock with a release of 21 million of 1.0 g juveniles.

catch of 100 t, which requires 156 raceways for growout. The total cost of production in raceways ranged from AUD\$1.00 million (M) to AUD\$1.34 M with a median of AUD\$1.20 M (Fig. 6). The enhanced catches were distributed almost normally (skewness = 0.57) with a median of 100 t, a standard deviation of 25 t and ranged from 23 to 244 t due to the uncertainties in various parameters (Fig. 7).

The revenue from the enhanced stock ranged from AUD\$0.26 million to AUD\$4.86 million (Fig. 8). The median revenue was AUD\$1.60 million. The difference between costs (hatchery, production, harvest, transport and release, and monitoring) and the revenue from enhancement varied between AUD\$-0.95 million and

AUD\$3.10 million, with a median of AUD\$0.22 million (Fig. 9), meaning on average that the enhancement would make a profit. There was 33.5% chance of losing money from the enhancement operation. It should also be noted that this index of "profit" does not include capital costs and their depreciation.

The wild catch ranged from 15 to 1527 t and had a skewed distribution with a mean of 406 t and a standard deviation of 216 t (Fig. 10). These estimates exhibit a wider range of catches than seen over the last 10–15 years in the Exmouth brown tiger prawn fishery (Fig. 2) but close to those recorded over the entire history of the fishery. Although the number of wild prawn larvae (1 g) was not a random variable in the simulation, the nat-

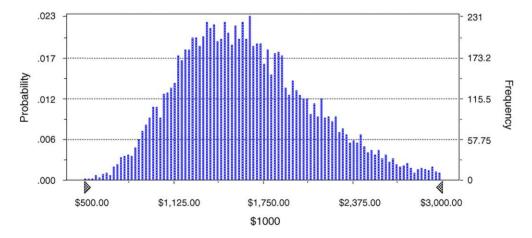


Fig. 8. Marginal revenue obtained from the catch of the enhanced stock.

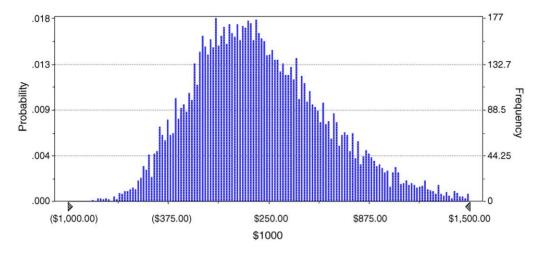


Fig. 9. Profit forecasts for the stock enhancement of 100 t enhanced catch.

ural mortality and growth from 1 g to recruitment to the fishery involved many stochastic factors. The large variation of wild catches proves how variable the recruitment to fishery can be simply due to the stochastic variation in early life stages as many fishery stock recruitment relationships show.

The largest contributor to the overall uncertainty of the enhanced prawn catch was the post-release mortality (53.6%), followed by the density-dependent mortality (17.0%), male  $L_{\infty}$  (12.6%), female  $L_{\infty}$  (6.4%), female k (5.1%), and male k (4.7%). All other parameters contributed less than 1% to the total variation in the forecast catch of enhanced prawns. These results suggest that post-release mortality and density-dependent

mortality are the largest factors affecting the success of stock enhancement.

# 4. Discussion

The simulation results suggest that a 100 t enhancement of *P. esculentus* stocks in Exmouth Gulf has a 66.5% chance of making a profit. Further, it is worth noting that the calculation of costs for grow-out in this study did not take into account the cost of capital investment required to build the grow-out raceways because the M.G. Kailis Group may offset these capital costs against its other aquaculture activities. Additional use

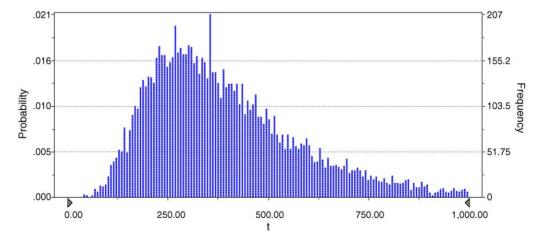


Fig. 10. Catch predictions for wild stock after the stock enhancement.

of the existing raceways for grow-out does not add extra costs to the company, which controls over 90% of the Exmouth Gulf tiger prawn fishery and will also be the major beneficiary of enhancement. In this very special case, the way to calculate costs and then profit can be justified, but for other normal enhancement projects, alternative costs of capital investment and depreciation on the capital must be included in the cost–benefit analysis.

The costs of monitoring enhancement included in this study was partial, specifically the cost of monitoring the contribution of the enhanced stock to the total catch assuming that the identification of enhanced from wild prawns by micro-satellite DNA loci is feasible and that a screening process can be developed (see Lehnert et al., 2003; Bravington and Ward, 2004). Under these assumptions, the costs of monitoring are not large, around AUD\$26,000 for the trial enhancement of 21 million juvenile prawns, mainly for obtaining adult prawns at sea and genetic analysis. This cost corresponds to the optimum monitoring level for an "average" fishing season. We defined optimum as the minimum number of samples required to obtain an estimate of the contribution of the enhanced stock to the total catch within 15% of its real value (with an 80% statistical power). In years of exceptionally high stock size (800 t), the statistical power of our sampling would drop to around 70%. Other costs of monitoring related to for example, potential changes in genetics of the wild stock and disease management have not been included in these costs.

This study assumed that all prawns were produced in one run, and, therefore, 156 raceways were required. The capital costs associated with building 156 raceways would be substantial - about AUD\$3.9 million. For economic efficiency, it would seem reasonable to produce the juveniles in two or three runs over a certain time period although the biological and ecological feasibility of such release strategies should be carefully studied. This is because the timing of release and the associated availability of the food required by the released stock are two critical factors in determining the probability of survival (Travis et al., 1998; Brown and Day, 2002). This is particularly important in the sub-tropical environment of Exmouth Gulf, where winter water temperatures fall below 15 °C. The current model is not capable of assessing the performance of multiple releases during a year, but a more generic model in the future should have this capability.

Size at release is another critical factor in determining the survival and cost of juvenile production. Given a certain production target, reducing the release size of the juveniles may lead to an increase in the number of juveniles needed for the release and the number of larvae for grow-out because releasing smaller prawns into the sea will increase the post-release mortality dramatically. This will increase the costs required for the production of larvae. The size at release should be determined based on a cost-effective analysis, producing a best combination between mortality and costs of seed production. This study also carried out a simulation which set the release size at 0.5 g. The post-release mortality rate from 0.5 to 1.0 g would be higher than in the optimally controlled grow-out environment. In the absence of data, the post-release mortality rate for 0.5 g juvenile P. esculentus was calculated by extending the length-dependent mortality for post 1 g juveniles to 0.5 g. The results from this simulation estimated that for a target production of 100 t of enhanced catch, 26 million 0.5 g juveniles would be required, which would need 75 raceways. The probability of making a profit for 0.5 g releases was 35%, only about half that when the release size of juveniles was 1.0 g. Although the costs in raceways decreased due to the shortened duration of the grow-out because of the smaller size at release, the total cost of post-larval production increased sharply with the need to produce 4 million more post-larvae.

In addition to the risk assessment, the sensitivity analysis also provided crucial information about the forecasts from the model. Post-release and density-dependent mortalities were identified as the largest factors affecting the enhanced prawn catch, followed by growth parameters. Those parameters that had the largest contribution to the overall uncertainty of model outcomes provide a potential focus for research to improve estimates of these parameters in the future and reduce the uncertainty in the model. It is worth mentioning that the uncertainty of an assumption depends on the type of distribution and the parameters of that distribution. If some assumptions in the model are changed, the uncertainty for a certain parameter might overcome the model sensitivity.

Density-dependent effects in marine populations are very case specific. If the density-dependent mor-

tality is strong, enhancement becomes the replacement of wild production with enhanced individuals rather than the enhancement of wild production (Hilborn, 1998), which is most likely when the wild population has reached its carrying capacity. One method of testing the extent of density-dependent effects is to carry out experiments of spatial controls, i.e. to have some sites enhanced and some un-enhanced. However, this is not possible in Exmouth Gulf and would be too costly in many instances. The philosophy behind this project is that the current production is wel 1 below the maximum sustainable level, and that releasing captive-raised juvenile prawns will use the existing levels of productivity of the marine environment, which may have been constrained to a low level by intensive fishing. If this is true, the intensity of this density dependence can be estimated from the density effects exhibited in stock recruitment relationship. The density-dependent mortality was estimated to be 7% at the current stock level, but the worst case could be 28% (Appendix A). A log-normal distribution was used in this study to account for the uncertainties. Density-dependent mortality depends on the relative competitive ability for food, habitat space, etc., which in turn is a function of individual size. We assumed that the enhanced prawns have the same size as the wild and that the density effect applies equally to both released and wild prawns  $(M_{1,\lambda} = M_{2,\lambda} = 0.5M_{\lambda})$ , in Table 1). If a multiple release strategy is adopted, the relative sizes of wild and enhanced prawns are not likely to be the same and it would be much more complex to estimate the magnitude of density effects.

The modelling reported in this study covers only one cycle from hatchery to capture. This is sufficient for a risk assessment designed to evaluate the feasibility of a full-scale enhancement for a short life species like *P. esculentus*. For a stock enhancement that is going to continue for many years, attention should be drawn to the influences of enhanced prawns left over from fishing on spawning stock size. If there is a clear positive effect on spawning stock size, enhancement may be needed only as a temporary tool to rebuild the stock. Regulation of fishing has an important role to play in protecting spawners even with stock enhancement in place.

This study developed a modelling framework to evaluate the performance of stock enhancement and the risk involved. The relatively low probability of making a profit was one of the major reasons for deciding not to progress to pilot scale enhancement (1–3 million juvenile *P. esculentus*) in the Exmouth brown tiger prawn fishery. This demonstrates the importance of bioeconomic analysis and risk assessment in stock enhancement. Such a modelling practice is applicable to any stock enhancement project and should be done before making the decision for a full-scale enhancement.

# Acknowledgements

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# Appendix A. Estimation of density-dependent mortality in the nursery grounds for juvenile *P. esculentus* in Exmouth Gulf, Australia

In the context of stock enhancement, density-dependent effects are likely to be a complex interaction between the carrying capacity of the environment and the stock levels of the enhanced and wild stocks. To quantify density-dependent effect after release, it is likely that large-scale, thus expensive, experiments would be necessary. An alternative to these experiments is to investigate the density effect exhibited in the stock—recruitment relationship of the wild stock and to calculate the post-release density-dependent mortality.

The relationship between spawning stock and recruitment can be described either with Ricker's (1954) or with Beverton–Holt's (1957) model. The density-dependent mechanisms in both models are very similar before recruitment reaches its peak. We, therefore, only use Ricker's model in this study,

$$\frac{R}{S} = \alpha e^{-\beta S} \tag{A.1}$$

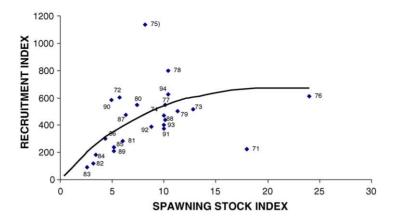


Fig. A.1. The stock recruitment relationship of the Exmouth Gulf tiger prawn stock (from Caputi et al., 1998).

were R is recruitment, S is spawning stock,  $\alpha$  and  $\beta$  are parameters. If there is no density dependence, i.e.  $\beta = 0$ , the recruitment per spawning stock should be constant  $(R/S = \alpha)$ , i.e. the number of recruits from one spawner remains the same regardless of the spawning stock size. However, as the density of recruits increases, competition is likely to take place between individuals for food and habitat. The most important impact of increased competition is an increase in natural mortality, although increased competition may have other impacts e.g. a decrease in growth rate (see Loneragan et al., 2001).

The increase in mortality rate reduces the survival rate of juveniles before recruitment, and consequently the recruits per unit spawning stock decreases. This density-dependent effect becomes more and more severe with the increasing number of recruits. The maximum R/S is  $\alpha$  in Eq. (A.1) when S approaches zero. So, the density-dependent effect can be estimated by comparing the value of R per S at its corresponding level of S with the value of  $\alpha$ .

Given the stock recruitment relationship in Eq. (A.1), the relative decrease, p, in recruits per unit spawning stock (R/S) caused by a certain proportion of increase,  $\zeta$ , in spawning stock due to enhancement can be calculated as follows:

$$p = \frac{R_0/S_0 - R_1/S_1}{R_0/S_0} = 1 - e^{-\beta \zeta S_0}$$
 (A.2)

where  $\zeta = (S_1 - S_0)/S_0$ , the subscript 0 represents the original levels of recruitment and corresponding spawning stock, and the subscript 1 represents the in-

creased levels of recruitment after enhancement and their corresponding spawning stocks.

When we try to enhance a wild stock, competition occurs between enhanced and wild stocks. If the released prawns have the same size as the wild counterparts and we assume that they have the same competitive ability, the density-dependent process will apply equally to both the enhanced and wild stocks. We can therefore treat the enhanced recruits as though they are a result of increasing the number of wild spawners. When the current recruitment level and the number of enhanced prawns to be released are known, the decrease in recruit per unit stock caused by the enhancement can be calculated on the basis of Eq. (A.2). Using the stock recruitment parameters to define density dependence of the enhanced stock, we assume that density-dependent processes operate between the size at which we release enhanced prawns and the size at which they recruit to the fishery. Given the length from release to recruitment into the fishery,  $T_{\lambda}$ , weekly density-dependent mortality rate,  $M_{\lambda}$ , can be estimated as follows,

$$M_{\lambda} = -\frac{1}{T_{\lambda}} \ln(1 - p) \tag{A.3}$$

The average annual catch over the last 10 years was about 400 t (Fig. 2), and its corresponding recruitment was 350 units (Fig. A.1). Catch is proportional to recruitment in a single cohort fishery that has a fixed duration of fishing season and a fixed number of boats. A 25% increase in catch demands the same percentage of increase in recruitment. Solving Eq. (A.1) gives  $S_0 = 5.3$  and  $S_1 = 7.2$ . The density-dependent mortality

caused by increased recruitment was then estimated to be 0.015 per week (p = 7.0%) based on Eq. (A.3). Several sources of uncertainty should be taken into account in the above calculation. The first and most immediate is the estimate of the recruitment corresponding to 400 t of catch. The closer recruitment is to its maximum level, the stronger the density dependence. If the recruitment corresponding to 400 t is actually 50% higher than our estimate of 350 units due to data noise, then the density-dependent mortality will rise to 0.066 per week (p = 28%, cf. Eq. (A.2)). This is a precautionary measure to prevent the underestimating of density-dependent process. The second is the uncertainty associated with the parameter estimates of the stock-recruitment relationship, which reflects observation errors in spawning stock and recruitment measurements and random environmental effects. To account for these uncertainties we used Monte Carlo method to randomly sample  $R_0$  from a uniform distribution between the two estimates of 350 units and  $1.5 \times 350$ units and  $\alpha$  and  $\beta$  from the normal distributions defined by the means and standard errors estimated from fishery data (Fig. A.1). The resulting  $M_{\lambda}$  (Eq. (A.3)) has a lognormal distribution with the logarithmic mean of -3.15 and the logarithmic standard deviation of 0.55. Given the assumption that density dependence has impact equally on both enhanced and natural prawns,  $M_{1,\lambda} = M_{2,\lambda} = 0.5 M_{\lambda}$ . This is only one example showing the calculation of the density-dependent effect when enhancement increases recruitment to the fishery by 25%. If the scale of stock enhancement changes, the density-dependent mortality needs to be re-estimated.

In the estimation of density-dependent mortality, we assumed that all the density dependence reflected in the *S/R* relationship happens between release and recruitment to fishery, at life stages older/bigger than the age/size of seeds. This is unlikely because density-dependent effects are likely to be more prevalent at the smallest lengths of settled post-larvae, when these are at the highest densities. Later as they grow their densities decrease rapidly, thus density dependence may be less important (Loneragan et al., 1994; Loneragan et al., 1998). This may suggest our estimates of density-dependent mortality may be biased high. In fact the idea of enhancement is exactly to reduce mortality during the phases where mortality is greatest and possibly density dependent.

# Appendix B. Estimation of the natural mortality rate in nursery grounds

O'Brien (1994) collected data of 12 cohorts of juvenile *P. esculentus* in Morton Bay, Queensland and estimated their mortality rates from settlement in and emigration out from nursery grounds. The estimated natural mortality rates range from 0.06 to 0.29 per week with a mean 0.16 ( $\pm S.D. 0.07$ ) per week. The average length at emigration is 16 mm CL and the length at settlement is around 2 mm. The data are not detailed enough to allow us to estimate the coefficients of Eq. (3).

However, the allometric relationship between natural mortality and body length is usually described as follows (Lorenzen, 2000):

$$M_{\rm L} = M_{\rm r} \left(\frac{L}{L_{\rm r}}\right)^{\xi} \tag{B.1}$$

where  $M_{\rm L}$  is the natural mortality rate at length L,  $M_{\rm r}$  is the natural morality rate at reference length  $L_{\rm r}$ , and  $\xi$  is the allometric exponent of the mortality and length relationship. After comparing seven release experiments (53 stocking events), Lorenzen (2000) concludes that the model with  $\xi = -1$  performs best.

With  $\xi = -1$ , Eq. (B.1) simplifies to  $M_L = M_r L_r / L$ . The mean natural mortality rate from settlement  $(L_r)$  to emigration  $(L_e)$  is then,

$$\bar{M} = \frac{1}{L_{\rm e} - L_{\rm r}} \int_{L_{\rm r}}^{L_{\rm e}} \frac{M_{\rm r} L_{\rm r}}{L} \, \mathrm{d}L = \frac{M_{\rm r} L_{\rm r}}{L_{\rm e} - L_{\rm r}} \ln \left(\frac{L_{\rm e}}{L_{\rm r}}\right)$$

From O'Brien (1994),  $\bar{M}=0.157$  per week,  $L_{\rm r}=2$  mm,  $L_{\rm e}=16$  mm, we can then calculate  $M_{\rm r}=0.529$  per week. Replacing  $L_{\rm r}$  and  $M_{\rm r}$  in Eq. (B.1) immediately leads to  $M_{\rm L}=1.05~{\rm L}^{-1}$ . This equation is the same as Eq. (3) when a=1.05 and b=-1. Usually b=-1 is quite consistent (Lorenzen, 2000). Our estimate of b=-0.99 for the grow-out period based on experimental data (Table 1) also supports Lorenzen's conclusion. We therefore contribute the uncertainty in natural mortality only to a with a standard deviation of 0.2.

Watson et al. (1993) use M = 0.065 - 0.042 per week for juvenile *P. esculentus* in their study on annual yield of the northern Queensland *P. esculentus* fishery. These values are much lower than the values we used in this study. Wang and Die (1996) use a constant natural mortality rate of 0.045per week for adult *P. esculen-*

tus greater than 26 mm in the study of the Australian northern prawn fishery. Using Eq. (B.1), we can easily estimate that M = 0.146per week for juveniles at 8 mm, less than half our value (M = 0.366 per week) for the juveniles of the same size. Although natural mortality may vary with environmental conditions, Lorenzen (1996) found no systematic differences between the mortality—weight (length) relationships determined for individual populations, species and fish in respective ecosystems. The relatively high length-dependent mortality rates we used for the post-release period may lead to conservative results for our simulations.

#### References

- Beverton, R.J.H., Holt, S.J., 1957. On the Dynamics of Exploited Fish Populations. Fisheries Investment, vol. 19. HMSO, London, 533 pp.
- Beyer, J.E., Kirchner, C.H., Holtzhausen, J.A., 1999. A method to determine size-specific natural mortality applied to westcoast steenbras (*Lithognathus aureti*) in Namibia. Fish. Res. 41, 133– 153.
- Blankenship, H.L., Leber, K.M., 1995. A responsible approach to marine stock enhancement. Am. Fish. Soc. Symp. 15, 167–175.
- Bravington, M.V., Ward, R.D., 2004. Microsatellite DNA markers: evaluating their potential for estimating proportions of wild-born and hatchery-reared offspring in an enhancement program. Mol. Ecol. 13, 1287–1297.
- Brown, C., Day, R.L., 2002. The future of stock enhancement: lessons for hatchery practice from conservation biology. Fish Fisheries 3, 79–94.
- Caputi, N., Penn, J.W., Joll, L.M., Chubb, C.F., 1998. Stock–recruitment–environment relationships for invertebrate species of Western Australia. In: Jamieson, G.S., Campbell, A. (Eds.), Proceedings of the North Pacific Symposium on Invertebrate Stock Assessment and Management, vol. 125. Canadian Special Publications in Fisheries and Aquatic Sciences, pp. 247–255.
- Crocos, P., Arnold, S., Sellars, M., Burford, M., Barnard, R., Mc-Culloch, R., 2003. Technology development for the high-density production of juvenile *Penaeus esculentus*. In: Loneragan, N.R., Kenyon, R.A., Crocos, P.J., Ward, R.D., Lehnert, S., Haywood, M.D.E., Arnold, S., Barnard, R., Burford, M., Caputi, N., Kangas, M., Manson, F., McCulloch, R., Penn, J.W., Sellars, M., Grewe, P., Ye, Y., Harch, B., Bravington, M., Toscas, P. (Eds.), Developing Techniques for Enhancing Prawn Fisheries, with a Focus on Brown Tiger Prawns (*Penaeus esculentus*) in Exmouth Gulf. CSIRO Marine Research, Australia, pp. 60–135.
- Gulland, J.A., 1983. Stock Assessment: A Manual of Basic Methods. Wiley, New York, 223 pp.
- Hannesson, R., 1993. Bioecnomic Analysis of Fisheries. Fishing News Books, London, 138 pp.
- Haywood, M.D.E., Vance, D.J., Loneragan, N.R., 1995. Seagrass and algal beds as nursery habitats for tiger prawns (*Penaeus semisul-*

- catus and P. esculentus) in a tropical Australian estuary. Marine Biol. 122, 213–223.
- Hilborn, R., 1998. The economic performance of marine stock enhancement projects. Bull. Marine Sci. 62, 661–674.
- Hilborn, R., Walters, C.J., 1992. Quantitative Fisheries Stock Assessment, Choice, Dynamics and Uncertainty. Chapman and Hall, London, 570 pp.
- Leber, K.M., 2002. Advances in marine stock enhancement: shifting emphasis to theory and accountability. In: Stickney, R.R., McVey, J.P. (Eds.), Responsible Marine Aquaculture. CAB International, pp. 79–90.
- Lehnert, S., Ward, R.D., Grewe, P., Bravington, M., 2003. Development and deployment of microsatellite markers. In: Loneragan, N.R., Kenyon, R.A., Crocos, P.J., Ward, R.D., Lehnert, S., Haywood, M.D.E., Arnold, S., Barnard, R., Burford, M., Caputi, N., Kangas, M., Manson, F., Mcculloch, R., Penn, J.W., Sellars, M., Grewe, P., Ye, Y., Harch, B., Bravington, M., Toscas, P. (Eds.), Developing Techniques for Enhancing Prawn Fisheries, with a Focus on Brown Tiger Prawns (*Penaeus Esculentus*) in Exmouth Gulf. CSIRO Marine Research, Australia, pp. 136–162.
- Loneragan, N.R., Kenyon, R.A., Haywood, M.D.E., Staples, D.J., 1994. Population dynamics of juvenile tiger prawns in seagrass habitats of the north-western Gulf of Carpentaria. Aust. Marine Biol. 119, 133–143.
- Loneragan, N.R., Kenyon, R.A., Staples, D.J., Poiner, I.R., Conacher, C.A., 1998. The influence of seagrass type on the distribution and abundance of postlarval and juvenile tiger prawns in the western Gulf of Carpentaria, Australia. J. Exp. Marine Biol. Ecol. 228, 175–196.
- Loneragan, N.R., Heales, D.S., Haywood, M.D.E., Kenyon, R.A., Pendrey, R.C., Vance, D.J., 2001. Estimating the carrying capacity of seagrass for juvenile tiger prawns (*Penaeus semisulcatus*): enclosure experiments in high and low biomass seagrass beds. Marine Biol. 139, 343–354.
- Loneragan, N.R., Crocos, P.J., Barnard, R.M., McCulloch, R.R., Penn, J.W., Ward, R.D., Rothlisberg, P.C., 2004. An approach to evaluating the potential for stock enhancement of brown tiger prawns (*Penaeus esculentus* Haswell) in Exmouth Gulf, Western Australia. In: Leber, K.M., Kitada, S., Blankenship, H.L., Svasand, T. (Eds.), Stock Enhancement and Sea Ranching: Developments, Pitfalls and Opportunities, 2nd ed. Blackwell Publishing, Oxford, pp. 444–464, Chapter 32.
- Loneragan, N.R., Kenyon, R., Crocos, P., Ward, B., Lehnert, S., Haywood, M., Arnold, S., Barnard, R., Bravington, M., Burford, M., Caputi, N., Kangas, M., McCulloch, R., Penn, J., Sellars, M., Manson, F., Harch, B., Ye, Y., Toscas, P., Grewe, P., 2003. Developing techniques for enhancing prawn fisheries, with a focus on brown tiger prawn (*Penaeus esculentus*) in Exmouth Gulf. CSIRO Marine Research, Australia, 281 pp.
- Lorenzen, K., 1996. The relationship between body weight and natural mortality in juvenile and adult fish: a comparison of natural ecosystems and aquaculture. J. Fish Biol. 49, 627–647.
- Lorenzen, K., 2000. Allometry of natural morality as a basis for assessing optimal release size in fish-stocking programmes. Can. J. Fish. Aquat. Sci. 57, 2374–2381.

- Munch, S.B., Mangel, M., Conover, D.O., 2003. Quantifying natural selection on body size from field data: winter mortality in Menidia menidia. Ecology 84, 2168–2177.
- Myers, R.A., Bowen, K.G., Barrowman, N.J., 1999. Maximum reproductive rate of fish at low population sizes. Can. J. Fish. Aquat. Sci. 56, 2404–2419.
- O'Brien, C.J., 1994. Population dynamics of juvenile tiger prawns *Penaeus esculentus* in south Queensland, Australia. Marine Ecol. Progr. Ser. 104, 247–256.
- Penn, J.W., Caputi, N., 1985. Stock recruitment relationships for the tiger prawn, *Penaeus esculentus*, fishery in Exmouth Gulf, West Australia, and their implications for management. In: Rothlisberg, P.C., Hill, B.J., Staples, D.J. (Eds.), Proceedings of the Second Australia National Prawn Seminar. NPS2, Australia, pp. 165–173.
- Penn, J.W., Caputi, N., 1986. Spawning stock recruitment relationships and environmental influences on the tiger prawn, *Penaeus esculentus*, fishery in Exmouth Gulf, West Australia. Aust. J. Marine Freshwater Res. 37, 491–505.
- Pepin, P., 1993. An appraisal of the size-dependent mortality hypothesis for larval fish: comparison of the multispecies study with an empirical review. Can. J. Fish. Aquat. Sci. 50, 2166–2174.
- Preston, N.P., Brennan, D.C., Crocos, P.J., 1999. Comparative costs of postlarval production from wild or domesticated Kuruma

- shrimp, *Penaeus japonicus* (Bate), broodstock. Aqua. Res. 30, 191–197
- Ricker, W.E., 1954. Stock and recruitment. J. Fish. Res. Board Canada 11, 559–623.
- Rothlisberg, P.C., Preston, N.P., Loneragan, N.R., Die, D.J., Poiner,
  I.R., 1999. Approaches to reseeding penaeid prawns. In: Howell,
  B., Moksness, E., Svasand, E. (Eds.), Stock Enhancement and Sea
  Ranching. Blackwell Science, Oxford, pp. 365–378, (672 pp).
- Travis, J., Coleman, F.C., Grimes, C.B., Conover, D., Bert, T.M., Tringali, M., 1998. Critically assessing stock enhancement: an introduction to the Mote symposium. Bull. Marine Sci. 62, 305–311.
- Wang, Y., Die, D., 1996. Stock–recruitment relationships of the tiger prawns (*Penaeus esculentus* and *Penaeus semisulcatus*) in the Australian northern prawn fishery. Marine Freshwater Res. 47, 87–95.
- Watson, R.A., Coles, R.G., Long, W.J.L., 1993. Simulation estimates of annual yield and landed values for commercial penaeid prawns from a tropical seasgrass habitat, northern Queensland, Australia. Aust. J. Marine Freshwater Res. 44, 211–219.
- White, T.F.C., 1975. Population dynamics of the tiger prawn *Penaeus esculentus* in the Exmouth Gulf prawn fishery, and implications for the management of the fishery. Ph.D. Thesis, University of Western Australia.