A COMPARTMENTAL MODEL OF THE EASTERN KING PRAWN FISHERY

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Introduction

Eastern king prawns (*Penaeus plebejus*) migrate north from estuaries along the coast of NSW and are subject to fishing pressure during this migration, chiefly from vessels operating north of Newcastle. They are also subject to fishing pressure by commercial and recreational fishers in the estuaries before migration. The proper management of this resource requires an understanding of this migration, and the consequences of harvesting individuals of different sizes and ages at different stages of their migration. Is it more profitable, for instance, to harvest prawns in the estuary before the migration, or catch fewer but larger prawns after they have left the estuary?

In an attempt to come to grips with these complex questions, we have been developing a simple model of the migration of prawns northwards along the NSW coast which allows simultaneous input of recruits from various estuaries through time, i.e. the recruitment in the model is allowed to be spatially distributed and to vary over time. Unfortunately little information is currently available on the relative contributions of estuaries to the overall recruitment, so initially we will be using the model as the basis of a yield per recruit model where recruitment is from a single region and at a single point in time. This would still allow questions to be considered, such as would it be profitable or not to the industry as a whole to close Botany Bay to prawn trawling.

The model is intended as a point of reference for future investigations. Currently it contains some gross simplifications. We do not have detailed information on how fishing pressure at any one place varies over time, although overall it is fairly steady through the year, so all parameters are taken as constant. Clearly, changes in weather conditions etc will mean that fishing pressure will vary. As we are using tag return data to estimate parameters, an important source of variability in the data is therefore being ignored. We do, however, allow fishing mortality to vary spatially, but the distribution of fishing mortality up and down the coast is assumed not to change over time.

Despite their lack of realism, constant parameter deterministic models have often provided robust approximations to the processes under study. Our model is constructed in the same spirit in the hope that it will provide a useful metaphor for the migration process. In this paper we give an abbreviated account of the model and discuss some of the inferences leading from it. A more complete discussion will be presented in Gordon *et al.* (submitted manuscript).

Our starting point has been the work of Glaister *et al.* (1990). In a yield per recruit study of prawns migrating across fishing grounds in northern NSW, Glaister *et al.* (1990) assumed that prawn populations in each fishing ground were reduced by natural and fishing mortality as well as emigration to the next fishing ground to the north through the action of constant instantaneous rates of natural and fishing mortality and a constant instantaneous emigration rate. This would imply an exponential decay in the population at each fishing ground. It was further assumed, however, that prawns moved across each fishing ground at a constant speed until they had passed the ground. Our approach is similar, in that we have assumed constant instantaneous rates of mortality and emigration. We have, however, made no separate movement assumption but have instead simply assumed that prawns emigrating from one fishing ground enter the next ground to the north. We have thus removed a possible logical inconsistency between the two movement assumptions. The immigration from one ground is matched with the emigration from the previous ground. The separate exponential decay models, one for each ground, thus have become a coupled system.

This type of model is known as a compartmental model (Anderson 1983). The NSW coast is divided into zones (or compartments). We have taken these to have constant latitudinal width. For each zone three parameters determine the dynamics of the system, namely the instantaneous rates of natural mortality, fishing mortality, and emigration to the next zone. Recruitment over time may be to any zone or distributed across several zones. The restriction to zones of constant width allows a hypothesis of a steady northward movement to be translated into one of a single instantaneous emigration rate for each zone. The simplifying assumption of a single instantaneous natural mortality rate, the same for each zone, also enables a restriction in the number of parameters. A further drastic reduction in the number of parameters is obtained by assuming the instantaneous fishing mortalities are known for each zone, up to a constant multiplier. This assumption is a useful starting point and it greatly reduces the number of parameters that have to be dealt with. For any assumed instantaneous rate of natural mortality there are now only two parameters, a single instantaneous rate of emigration from each zone and another parameter, essentially a catchability parameter, which is a multiplier of an assumed set of fishing efforts or instantaneous fishing mortalities for each zone.

The model

We first consider the model without the simplifications which reduce the number of parameters. For the sake of reducing the number of equations we have to write down we shall take the number of zones to be four, but the mathematics is the same for any number of zones. The actual number of zones used depends on the width assumed for each zone and the stretch of coast to be covered. Prawns are assumed to be sufficiently well dispersed in a zone for the instantaneous rate of departure to the next zone to be proportional to the number in the zone. For this to be approximately true the zones have to be small. On the other hand, for the model to be computationally manageable and for there to be a reasonable correspondence between zones and fishing grounds, the number of zones should not be too large.

Note that the interpretation of the instantaneous emigration rate can only be made in terms of a particular arrangement of zones. The width of a zone is in effect a hidden parameter of the system which governs the degree to which prawns disperse as they migrate. This aspect of the model has not yet been investigated. Our arrangement of zones has been made on purely pragmatic grounds, and there is no claim that it is an optimal arrangement. We have taken 21 zones for the coast from Jervis Bay on the south coast to the Queensland border, of 20 nautical miles width, the 22nd zone being Queensland.

Suppose the number of prawns at time t in the i^{th} zone is $x_i(t)$, so that the population of prawns at time t is described by the vector $\mathbf{x}(t)$, where $\mathbf{x}'(t) = (x_1(t), x_2(t), ...)$. Suppose the instantaneous rate of emigration from zone i to zone $i+1$ is λ_i, and the instantaneous mortality in zone i is μ_i, where $\mu_i = \mu_i^{(1)} + \mu_i^{(2)}$, the natural and fishing mortality rates respectively. Write $\kappa_i = \lambda_i + \mu_i$. Then in a small time interval δt, the number of prawns moving to the $(i+1)^{th}$ zone is $\lambda_i x_i(t)\delta t$ and the number dying is $\mu_i x_i(t)\delta t$. Hence,the behaviour of the system is described by a system of coupled first order linear differential equations.

$$
\begin{aligned}
\frac{dx_1}{dt} &= -\kappa_1 x_1 \\
\frac{dx_2}{dt} &= \lambda_1 x_1 - \kappa_2 x_2 \\
\frac{dx_3}{dt} &= \lambda_2 x_2 - \kappa_3 x_3 \qquad (1) \\
\frac{dx_4}{dt} &= \lambda_3 x_3 - \kappa_4 x_4
\end{aligned}
$$

This system may be written simply in matrix terms. Writing

$$
A = \begin{pmatrix} -\kappa_1 & 0 & 0 & 0 \\ \lambda_1 & -\kappa_2 & 0 & 0 \\ 0 & \lambda_2 & -\kappa_3 & 0 \\ 0 & 0 & \lambda_3 & -\kappa_1 \end{pmatrix}
$$

where $\lambda_i > 0$, $\kappa_i > 0$, equations (1) may be written.

$$\frac{d\mathbf{x}}{dt} = A\mathbf{x}$$

The notation has been chosen to coincide with that of Gordon *et al.* (1970), in which a similar catenary compartmental model was used in another context. The usual parameters *F* and *M* for instantaneous fishing and natural mortality have not been used as they would be confusing in a matrix context, in which capital letters are customarily reserved for matrices. The Greek letter λ (lambda) is widely used for a rate parameter, while μ (mu) is commonly used for a mortality parameter in many contexts. The two types of mortality occurring are distinguished by a superscript.

If the initial state of the system is given by $\mathbf{x}(0)$, the solution of the system is

$$\mathbf{x}(t) = e^{At}\,\mathbf{x}(0).$$

In the case of a single release of N tagged prawns at time $t = 0$ from zone 1, $\mathbf{x}'(0) = (N,0,0,\ldots)$, and $\mathbf{x}(t)$ is N times the first column of e^{At}.

The matrix e^{At} is known as the exponential of the matrix At (Braun 1983). It may be expanded in a series form in the same way as the familiar exponential function

$$e^{At} = I + At + \frac{1}{2!}A^2t^2 + \ldots + A^n\frac{t^n}{n!} + \ldots$$

The matrix exponential exists for any matrix A, and any t and satisfies the equation

$$e^{A(t+s)} = e^{At}\,.\,e^{As}$$

for any scalars t, s, and so generalises an important property of the familiar exponential function. This multiplicative property can be used to discretize the system. Suppose time is measured in multiples of a time unit Δt. Then measuring time in weeks, ie. taking $\Delta t = 1$ week,

$\mathbf{x}(1) = e^{A\Delta t}\,\mathbf{x}(0) \quad = e^{A}\,\mathbf{x}(0)$,

$\mathbf{x}(2) = e^{A(2\Delta t)}\,\mathbf{x}(0) \quad = e^{A}.\,e^{A}\,\mathbf{x}(0)$, etc.

Writing $P = e^{A}$,

$\mathbf{x}(1) = P\,\mathbf{x}(0)$,

$\mathbf{x}(2) = P\,\mathbf{x}(1) = P^2\,\mathbf{x}(0)$,

$\mathbf{x}(3) = P\,\mathbf{x}(2) = P^2\,\mathbf{x}(1) = P^3\,\mathbf{x}(0)$,

so stepping through time amounts to repeated multiplication by the system matrix *P*, giving the state vector **x** in successive weeks.

Catches

The catch rate at time t in each zone depends on the number of prawns vulnerable to fishing in the zone, and the instantaneous rate of fishing mortality in the zone, $\mu_i^{(2)}$. Catches thus depend directly on the solution $\mathbf{x}(t)$ of the above system.

Let $\mathbf{y}(t)$ be the cumulative catch vector at time t, ie.

$$\mathbf{y}'(t) = (y_1(t), y_2(t), ...)$$

where $y_i(t)$ is the cumulative catch at time t in the i^{th} zone.

Then

$$\frac{dy_1}{dt} = \mu_1^{(2)} x_1 \text{, for zone 1,}$$

$$\frac{dy_2}{dt} = \mu_2^{(2)} x_2 \text{, for zone 2, etc.}$$

Let $M^{(2)}$ be a matrix whose i^{th} diagonal term is $\mu_i^{(2)}$, and whose off-diagonal terms are all zero, $M^{(2)} = \text{diag}\,(\mu^{(2)})$.

The equations determining the catches may then be written

$$\frac{d\mathbf{y}}{dt} = M^{(2)}\mathbf{x}\,. \qquad (2)$$

By a straight forward integration it is found that

$$\mathbf{y}(t) = M^{(2)} A^{-1} (e^{At} - I)\, \mathbf{x}(0)\,,$$

and that the catch taken in the time interval $(k, k+1)$ is

$$\mathbf{y}(k+1) - \mathbf{y}(k) = M^{(2)} A^{-1} (e^{A} - I)\, \mathbf{x}(k)$$

$$= B\, \mathbf{x}(k) \quad \text{say},$$

where $B = M^{(2)} A^{-1} (e^{A} - I)$.

This is a direct generalization of the familiar Baranov catch equation. In the usual notation, with instantaneous fishing mortality F and total instantaneous attrition rate Z (which may include loss by emigration as well as rate mortality), the cumulative catch $y(t)$ at time t from an initial population N at time 0 is

$$y(t) = \frac{FN}{Z}(1 - e^{-Zt})\,.$$

Thus the matrix $M^{(2)}$ is the analogue of F, $\mathbf{x}(0)$ is the analogue of N, the matrix $-A^{-1}$ is the analogue of the reciprocal $\frac{1}{Z}$, while the matrix exponential e^{At} is the analogue of the term e^{-Zt}.

As t tends to ∞, cumulative catch in the familiar (one zone) case tends to $\frac{FN}{Z}$. In the matrix case, it can be shown that the matrix exponential term vanishes, and

$$\mathbf{y}(t) \rightarrow -M^{(2)} A^{-1}\, \mathbf{x}(0)\,.$$

Cumulative numbers dying of natural causes in each zone can be found simply by changing the type of mortality, ie. by replacing $M^{(2)} = \text{diag}\,(\mu^{(2)})$ by $M^{(1)} = \text{diag}\,(\mu^{(1)})$ in (2), while cumulative numbers leaving the zones can be found by replacing $M^{(2)}$ by $\Lambda = \text{diag}\,(\lambda)$. Limiting expressions similar to the one given above also hold.

Solution of equations

Explicit expressions for the solutions $e^{At}\,\mathbf{x}(0)$ and for A^{-1} can be found (see Gordon *et al.* 1970). It turns out, however, that on a computer, the matrix exponential can be calculated easily from the series

$$P = e^{A} = I + A + \frac{A^2}{2!} + \frac{A^3}{3!} + \ldots..,$$

and the catches can be found from the expansion

$$A^{-1}(e^{A} - I) = I + \frac{A}{2!} + \frac{A^2}{3!} + \ldots..$$

at the same time. With a time period of 1 week, and double precision arithmetic, we have obtained results for the parameter ranges we encounter, accurate to better than single precision arithmetic. The number of terms needed depends on the parameter values and the accuracy desired.

Estimation of parameters

The system of differential equations we have used is linear, but the solutions as functions of the parameters are non-linear. Suppose after reparameterizing the system as discussed above, the parameter vector is θ and the catch obtained from zone j in week i as a function of θ is $f_{ij}(\theta)$. Suppose in a tagging experiment the number of prawns caught in zone j during week i is x_{ij}. Then a least squares estimate of θ is found by minimizing

$$\sum_{i,j}(x_{ij}-f_{ij}(\theta))^2$$

over admissible θ. We have used tags returned within 60 weeks of release recaptured in NSW (a few returns from Queensland have been ignored). Data from the closure period after tags were released in the release zone were also excluded, except to adjust for tags removed in the closure period.

Yield per recruit extension of the model

For reasons of space, only a brief summary of how the model can be extended to a yield per recruit model can be given. Given N prawns released in a given zone, and parameter vector θ, the catches in each zone for each subsequent week can be calculated. Using published age-length and length-weight relationships (Glaister *et al.* 1987), assuming a given age (or length) at release, weights of catches can be calculated. This is done by integrating the weight-age relationships numerically (Simpson's rule) to find the average weight of a prawn by zone and time (age), and then multiplying by the numbers caught predicted by the model, again for all zones and time periods (weeks). The assumed age-length relationships were $W = 0.0004L^{3.1159}$ for males, and $W = 0.0006L^{2.9818}$ for females, where W is weight in grams and L length in mm. The von Bertalanffy parameters used were $L_\infty = 45.44$ mm for males and 59.53 mm for females, with $K = 0.0595$ week^{-1} for males and 0.0483 week^{-1} for females. The sexes were assumed to be in equal proportions. All prawns are vulnerable to capture after migration, so size selectivity does not have to be introduced. The size of a prawn when recruited to the ocean fishery, determines the parameter t_0. Instantaneous natural mortality of 0.06 week^{-1} was assumed for untagged prawns. Management questions can be resolved by comparing the yield of catches in estuaries with the expected yields from the ocean model, over a range of recruit sizes, assuming the estuary catch is foregone.

Results

Boat registrations at each port (Figure 1) have been used to provide initial instantaneous fishing mortality estimates at each zone, scaled to correspond to a value of 0.0451 week^{-1} for 55 boats, the best estimate available in the literature (Glaister *et al.* 1990). Using the restricted parameterization two parameters have been estimated for a range of assumed natural mortality rates, namely a common λ and a common multiplier q for the instantaneous fishing mortality estimate. The value $q = 1$ corresponds to an instantaneous fishing mortality of 0.00082 week^{-1} per boat in each zone, (ie 0.0451 week^{-1} for 55 boats). Actual and predicted tag returns from the model for a single tag release are shown in Tables 1 and 2 respectively. The fit of the model is shown in Table 3 for various assumed natural mortality rates. The number of prawns predicted to be caught was close to the number of tags returned when instantaneous natural mortality was 0.1 (Table 4). The parameter estimates for this value of $\mu^{(1)}$ were $\lambda = 0.30585$ week^{-1} and $\hat{q} = 0.88827$. However this assumed natural mortality includes tag loss, which in a recent 12 week study in Botany Bay was estimated to be 0.033 week^{-1}. The difference, 0.067 week^{-1}, is consistent with the value of 0.062 week^{-1} for instantaneous natural mortality estimated by Glaister *et al.* (1990).

Preliminary results of yield per recruit analyses have suggested that growth of recruits from

Botany Bay to the ocean fishery during their migration does not compensate for the mortality they experience during the migration. Using the size distribution of catches in Botany Bay (average size 21 mm), and converting to a weight distribution, the average weight of 1000 prawns caught in Botany Bay is 5.43 kg. If 1000 prawns of size 25 mm are recruited to the ocean fishery, the total yield given by the model is only 3.70 kg. Consideration of economic yield per recruit reinforces this conclusion, as king prawns from Botany Bay, though small, fetch relatively high prices because of market freshness. For estuaries farther north, with shorter migrations and lower prices, conclusions could well be different.

Discussion

The model has provided a way of comparing different tag releases, and assessing the relative influence of tag returns from different zones. Fits need to be improved, so there is a need for better data, particularly fishing effort data as it varies over time at a good level of spatial resolution, and a corresponding need to extend the model to incorporate this information. This can be done within the framework of the current model by allowing time-varying parameters to be piecewise constant. Estimates of recruitment by estuary are also needed for a proper understanding of the fishery. Nevertheless, even with effort data by zone that probably was only a rough approximation to the number of boats actually fishing, and a restricted parameterization, the results indicate that the model has been able to capture successfully the broad features of the migration process.

Note that many of the results quoted do not make use of the particular form of the matrix A, so the approach adopted potentially extends to other migration problems or other arrangements of zones with different connectivities (eg. offshore / onshore divisions as well).

The development of a model in which the emigration rate has an interpretation independent of the zonal arrangement would be desirable. This could be a diffusion type model, using partial differential equations rather than ordinary differential equations, and finite element techniques. It is planned to extend the model to include estuaries and factors affecting prawn production of estuaries. In the meantime it is hoped that the compartmental model we have adopted provides a useful generalization of an old fishery model.

Acknowledgements

We are grateful to Dr Derek Staples, Professor Tony Underwood and Mr Ian Somers for helpful discussions. We particularly thank Dr Keith Sainsbury and colleagues at C.S.I.R.O. Hobart for discussions and advice during the early stages of the project, and Dr Robert Kearney for facilitating these contacts. We also thank Penny Brett, Duncan Worthington and Nokome Bentley for assistance in preparing the manuscript.

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Table 1. Tag Returns (a single release of 2587 prawns near Newcastle, December 1991).

	Zone														
Weeks	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
1		18													
2		13													
3		11													
4		3													
5		1													
6		11													
7		3													
8		5													
9	2	2													
10		1													
11		6													
12		4													
13		5			1										
14		10			1										
15		4			1										
16	1	3													
17		3													
18		2			1					1					
19		1			4					1					
20					2										
21					1				1						
22		4			1										
23		1			1										
24															
25											1				
26										1					
27															
28												1			
29												1			
30										1					
31														1	
32											1		1		
33															
34															
35															
36															
37												1			
38										1					
39															
40															

Note: 1 Prawn was caught in week 53, zone 16.

Shading denotes closure period

Table 2. Predicted Tag Returns (assuming $\mu^{(1)} = 0.1$ and fitting over 60 weeks).

	Zone														
Weeks	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
1		4.4	0	0											
2		9.2	0.4	0.1	0										
3		10.2	0.8	0.4	0										
4		9.5	1	0.6	0.1	0									
5		8.1	1.1	0.9	0.2	0									
6		6.5	1.1	1.1	0.3	0		0							
7		5.1	1	1.2	0.4	0		0	0						
8		3.9	0.9	1.2	0.5	0		0	0	0					
9	1.2	2.9	0.8	1.2	0.5	0.1		0	0	0					
10	0.8	2.2	0.6	1.1	0.6	0.1		0.1	0	0	0				
11	0.5	1.6	0.5	1	0.6	0.1		0.1	0.1	0	0				
12	0.3	1.1	0.4	0.8	0.5	0.2		0.2	0.1	0.1	0	0			
13	0.2	0.8	0.3	0.7	0.5	0.2		0.2	0.2	0.2	0	0			
14	0.1	0.6	0.2	0.6	0.4	0.1		0.2	0.2	0.2	0.1	0			
15	0	0.4	0.2	0.5	0.4	0.1		0.3	0.3	0.3	0.2	0			
16	0	0.3	0.1	0.4	0.3	0.1		0.3	0.3	0.3	0.2	0	0		
17	0	0.2	0.1	0.3	0.3	0.1		0.3	0.3	0.4	0.3	0.1	0		
18	0	0.1	0	0.3	0.2	0.1		0.3	0.4	0.4	0.3	0.1	0		
19	0	0	0	0.2	0.2	0		0.3	0.4	0.4	0.4	0.2	0	0	
20	0	0	0	0.2	0.2	0		0.3	0.4	0.5	0.4	0.2	0	0	
21		0	0	0.1	0.1	0		0.3	0.4	0.5	0.4	0.2	0	0	0
22		0	0	0	0.1	0		0.2	0.4	0.5	0.5	0.3	0	0	0
23		0	0	0	0	0		0.2	0.3	0.5	0.5	0.3	0	0	0
24		0	0	0	0	0		0.2	0.3	0.5	0.5	0.3	0	0	0
25		0		0	0	0		0.2	0.3	0.5	0.5	0.3	0	0	0
26				0	0	0		0.2	0.3	0.4	0.5	0.3	0	0	0
27				0	0	0		0.1	0.2	0.4	0.5	0.3	0	0	0
28				0	0	0		0.1	0.2	0.4	0.5	0.3	0	0	0
29				0	0	0		0	0.2	0.4	0.4	0.3	0	0	0
30					0	0		0	0.2	0.3	0.4	0.3	0	0	0
31					0			0	0.1	0.3	0.4	0.3	0	0	0
32								0	0.1	0.3	0.3	0.3	0	0	0
33								0	0.1	0.2	0.3	0.3	0	0	0
34								0	0	0.2	0.3	0.2	0	0	0
35								0	0	0.2	0.2	0.2	0	0	0
36								0	0	0.1	0.2	0.2	0	0	0
37								0	0	0.1	0.2	0.2	0	0	0
38								0	0	0.1	0.2	0.2	0	0	0
39								0	0	0	0.1	0.1	0	0	0
40								0	0	0	0.1	0.1	0	0	0

Note: 0 indicates a value> 0.01 but <0.1. Blank indicates a value <0.01. Weeks greater than 40 are omitted.

Table 3. Ordinary sum of squares fits: $\mu^{(1)}$ assumed, λ and q estimated.

Run #	$\mu^{(1)}$	λ	SE(λ)	q	SE(q)	Cor(λ,q)	Res Mean Sq	Res Sum Sq	Total Sum Sq
1	0.02	0.150	0.006	0.353	0.018	0.112	0.816	726.224	1063
2	0.04	0.192	0.007	0.528	0.023	0.141	0.723	643.216	1063
3	0.06	0.227	0.009	0.669	0.027	0.128	0.674	600.088	1063
4	0.08	0.260	0.011	0.784	0.030	0.100	0.651	579.175	1063
5	0.1	0.306	0.014	0.888	0.033	0.077	0.636	566.035	1063
6	0.12	0.371	0.016	0.988	0.036	0.073	0.623	554.187	1063
7	0.14	0.439	0.019	1.083	0.038	0.075	0.609	541.801	1063
8	0.16	0.497	0.021	1.173	0.040	0.077	0.595	529.548	1063
9	0.18	0.544	0.023	1.257	0.042	0.077	0.582	518.282	1063
10	0.2	0.581	0.025	1.336	0.044	0.074	0.571	508.409	1063

Table 4. Predicted and actual tags returned by zone (60 weeks), for different natural mortality assumptions.

	Zone														
Run#	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	Total
1	21.75	74.37	13.02	19.76	12.16	4.14	0.00	10.90	15.35	21.56	21.23	12.99	2.36	1.48	1.16	232.22
2	14.48	76.47	12.57	17.97	10.51	3.46	0.00	9.11	13.35	20.00	21.44	14.62	3.07	2.25	2.10	221.40
3	9.61	75.10	11.79	16.10	9.00	2.84	0.00	6.96	9.98	14.77	15.86	11.01	2.40	1.87	1.87	189.16
4	6.22	71.94	10.92	14.42	7.80	2.38	0.00	5.47	7.63	11.01	11.60	7.96	1.73	1.36	1.39	161.84
5	3.49	67.46	10.10	13.15	7.01	2.11	0.00	4.72	6.49	9.28	9.71	6.62	1.44	1.14	1.17	143.89
6	1.62	62.40	9.37	12.25	6.56	1.98	0.00	4.45	6.16	8.87	9.36	6.45	1.41	1.12	1.17	133.15
7	0.75	58.40	8.80	11.55	6.21	1.88	0.00	4.26	5.92	8.58	9.13	6.34	1.39	1.11	1.17	125.49
8	0.38	55.67	8.37	10.97	5.89	1.78	0.00	4.02	5.58	8.08	8.61	5.98	1.31	1.05	1.10	118.78
9	0.22	53.81	8.04	10.47	5.58	1.67	0.00	3.74	5.15	7.43	7.87	5.44	1.19	0.94	0.98	112.53
10	0.14	52.50	7.77	10.02	5.29	1.57	0.00	3.44	4.69	6.70	7.04	4.82	1.04	0.82	0.85	106.67
Tags returned	3	111			13				1	6	2	3	1	1		141
Boats registered	20	20	4	7	5	2	0	8	15	30	45	44	13	14	20	
$\mu^{(2)}$ for q=1* (week^{-1})	0.0164	0.0164	0.00328	0.00574	0.0041	0.00164	0.0	0.00656	0.0123	0.0246	0.0369	0.03608	0.01066	0.01148	0.0164	

*Reference instantaneous fishing mortality obtained by multiplying number of boats registered by 0.00082 corressponding to an instantaneous fishing mortality of 0.0451 for 55 boats for the Clarence River (Glaister *et al.* 1990) The actual instantaneous fishing mortalities used in the model are found for each run by multiplying these values by q , given together with λ value in Table 3.

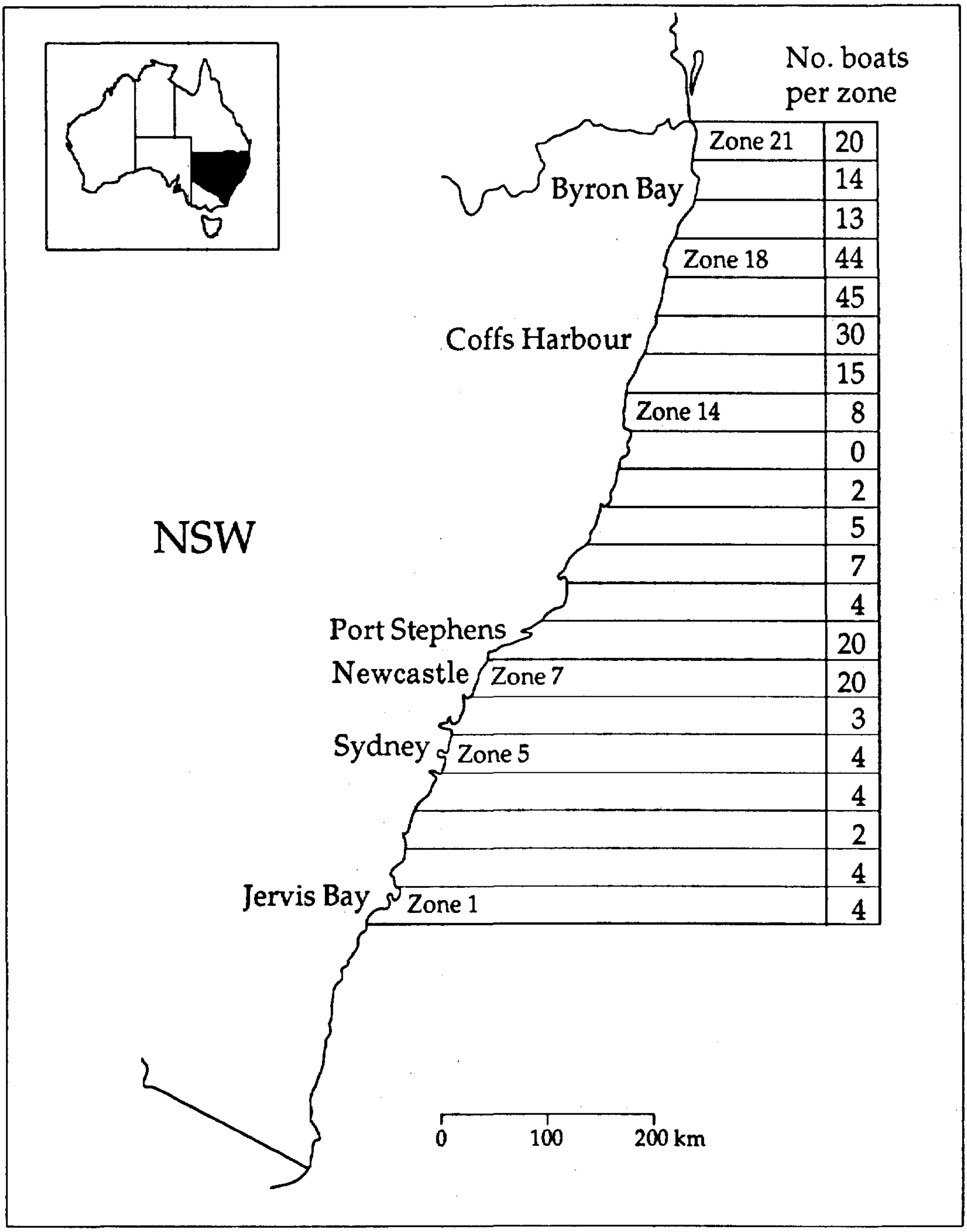

Figure 1. Arrangement of zones and number of registered fishing vessels per zone.