Estimating the size-transition matrix
for Tasmanian rock lobster, *Jasus edwardsii*

André E. Punt[A], Robert B. Kennedy[B] and Stewart D. Frusher[B]

[A]*CSIRO Division of Marine Research, GPO Box 1538, Hobart, Tas. 7001, Australia. email: a.punt@ml.csiro.au*
[B]*DPIF Division of Marine Resources, Marine Research Laboratories, Taroona, Tas. 7053, Australia*

Abstract.   Assessment of the southern rock lobster (*Jasus edwardsii*) resource in Tasmania is based on a size-structured population dynamics model. One of the most important inputs to this model is the set of matrices that represent the season-specific probabilities of a lobster growing from one size-class to another. These matrices are estimated from tag–recapture data within a maximum-likelihood estimation framework. Measures of precision are determined from the asymptotic variance–covariance matrix. Various alternative models are contrasted for one site in the south-east of Tasmania, and a best model is selected by the likelihood ratio test. The growth model used is based on a generalization of the von Bertalanffy growth equation. Growth rates differ markedly among regions around Tasmania, being slowest in the south and fastest in the north. Growth of legal-size males is noticeably faster than that of legal-size females. It is shown that ignoring the effects of selectivity can lead to biased estimates of growth rate. An extension to the method is presented and applied that estimates size-specific selectivity in an attempt to eliminate this bias.

Introduction

In many invertebrate marine species, individual animals cannot be aged. This is because they lack known annuli. Stock assessments for invertebrate species have, in the past, had to be based on methods that do not require information about growth rates, such as production models (e.g. Saila *et al.* 1979). More recently, however, size-structured stock assessment methods that do not require an explicit relationship between size and age have been applied to invertebrates (e.g. Bergh and Johnston 1992; Johnston and Bergh 1993; Zheng *et al.* 1995; Punt and Kennedy 1997). The ability of these stock assessment methods to make quantitatively reliable predictions depends crucially on knowledge of growth rates. Traditionally, growth of invertebrates has been modelled by deterministic relationships (often the von Bertalanffy growth equation) parameterized with the aid of data from tag–recapture studies (e.g. McKoy and Esterman 1981; Annala and Bycroft 1988). Such relationships are, however, inadequate for use in size-structured modelling exercises because of the need to describe both average growth rates and individual variation in these rates.

Punt and Kennedy (1997) assess the southern rock lobster (*Jasus edwardsii*) resource off Tasmania, Australia, with the aid of a size-structured model and make predictions about the risk related to various alternative levels of future catch. Growth is represented in the model through sex- and season-specific size-transition matrices. The representation of growth in this manner is common when size-structured stock assessment methods are applied

(e.g. Sainsbury 1982; Sullivan *et al.* 1990; Bergh and Johnston 1992).

The entries in the size-transition matrix, $P_{i,j}$, represent the probability that an animal in size-class *j* will grow into size-class *i* during the current model time-step. This way of modelling growth ignores the possibility that some individuals are genotypically or environmentally disposed to fast or slow growth and assumes instead that the current size of an individual is the sole determinant of its growth. On the assumption that rock lobsters do not shrink, the size-transition matrix has a lower-triangular form:

$$\mathbf{P} = \begin{bmatrix} P_{1,1} & 0 & . & 0 & 0 \\ P_{2,1} & P_{2,2} & . & 0 & 0 \\ . & . & . & 0 & 0 \\ P_{x-1,1} & P_{x-1,2} & . & P_{x-1,x-1} & 0 \\ P_{x,1} & P_{x,2} & . & P_{x,x-1} & P_{x,x} \end{bmatrix}, \qquad (1)$$

where *x* is the largest size-class considered in the model. The $P_{i,j}$ need to be selected so that the constraint $\sum_{i=j}^{x} P_{i,j} = 1$ is satisfied.

The use of a size-transition matrix to describe growth differs from conventional descriptions of growth for crustaceans, which tend to focus on the moult increment and the intermoult period (e.g. Annala and Bycroft 1988; Fogarty and Idoine 1988). The size-transition matrix approach is more appropriate for size-structured modelling because it considers size-class rather than size itself as the

basic measure of length and because it allows for the case in which an animal moults but remains in its current size-class. Thus, the population dynamics model used for assessment purposes defines growth as growing from one size-class to another.

This paper outlines a method for describing growth by means of a size-transition matrix and develops an estimation framework that uses tag–recapture data. The method is applied to the populations of southern rock lobster off Tasmania. The model developed in this paper considers average growth patterns and their variation explicitly. It also considers the possible impact of selectivity on growth rate estimation. If the probability of recapture increases with size, the probability of recapturing an animal that has grown substantially will exceed that of an animal of the same original size that has

Fig. 1. Tasmania, showing the eight statistical areas.

not grown. Intuitively, this will lead to positive bias in the estimated growth rates and to over-optimistic management advice.

Analyses are conducted separately for four of the eight statistical areas around Tasmania (Fig. 1). For ease of presentation, most of the results are shown for Area 2 (southeast-central Tasmania) only.

Materials and methods

Data collection

Lobsters were tagged by inserting individually numbered tags (T-bar anchor tags, Hallprint Pty Ltd, Holden Hill, SA) ventrally in the first abdominal segment. At tagging and recapture, lobsters were sexed and measured. Data on time and location were recorded along with information about the data provider (scientist, fisher, etc.). Females were further checked for maturity (presence or absence of setose pleopods) and reproductive state (presence or absence of ova on setae). Information on

moulting is available for some of the tagged lobsters, which had a pleopod clipped at tagging.

Length is expressed in terms of carapace length (CL)—the dorsal measurement of the carapace from between the basal plates of the antennae to the posterior edge of the carapace. Carapace length was measured to the nearest millimetre with calipers.

Modelling and parameter estimation

The purpose of the model is to estimate the entries in the size-transition matrix. The entries in this matrix are likely to depend on statistical area, season and sex because of spatial, seasonal and sex-specific growth characteristics (e.g. Annala and Bycroft 1988). The variant of the model used to describe size-transition for the case in which growth occurs instantaneously is presented first, followed by a description of the likelihood function maximized to estimate values for the model parameters for this case. The extensions necessary to allow for differential probabilities of recapture (selectivity) and continuous growth, tagging and recapture are then given. The model has the flexibility to incorporate several functional forms to represent average growth and variation about that average. The choices considered in this paper for these forms are provided. For ease of presentation, the dependence on area and sex is ignored, and that on season is ignored until the extensions needed to allow for continuous growth are presented. Ignoring the dependence on area and sex is a trivial omission for this paper because the model is fitted to data for each area and sex separately.

The data are analysed on the basis of 2-mm size-classes. This choice of size-class is a compromise between the desire for very small size-classes to improve the resolution of the population dynamics model used for assessment purposes and the desire for large size-classes to simplify the calculations and avoid biases caused by measurement error. Some records were excluded for reasons given in Table 1.

Some tagged animals have been recaptured several times (Table 1). Inclusion of these animals in the analyses would lead to underestimation of growth. Consider the case of a fisher recapturing an animal that, when it was released, was just below the minimum size. If the animal did not grow, it
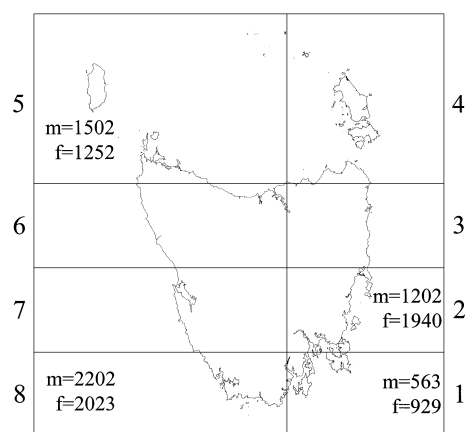
Table 1. Summary of the available tagging data
The column 'Unique' shows the number of lobsters that have been recaptured at least once and the column 'Multiple' the number of multiple recaptures. The total number of recaptures is the sum of the entries in the columns 'Unique' and 'Multiple'. The column 'Excluded' lists the number of records excluded from the analyses of this paper

Area	Sex	Releases	Recaptures		
			Unique	Multiple	Excluded[A]
1	Male	3707	630	484	67
	Female	4526	1022	977	93
2	Male	7385	1455	1002	253
	Female	12069	2386	2293	446
5	Male	7241	1656	262	154
	Female	7859	1448	249	196
8	Male	9570	2437	1414	235
	Female	8099	2393	1406	370
Total	Male	27903	6178	3162	709
	Female	32553	7249	4925	1105

[A]Without complete information on date, size and location of release and recapture, or with sex unknown, or with lengths outside the range 60–200 mm, recaptured in the same three-month period in which they were released, or at liberty for more than two years.
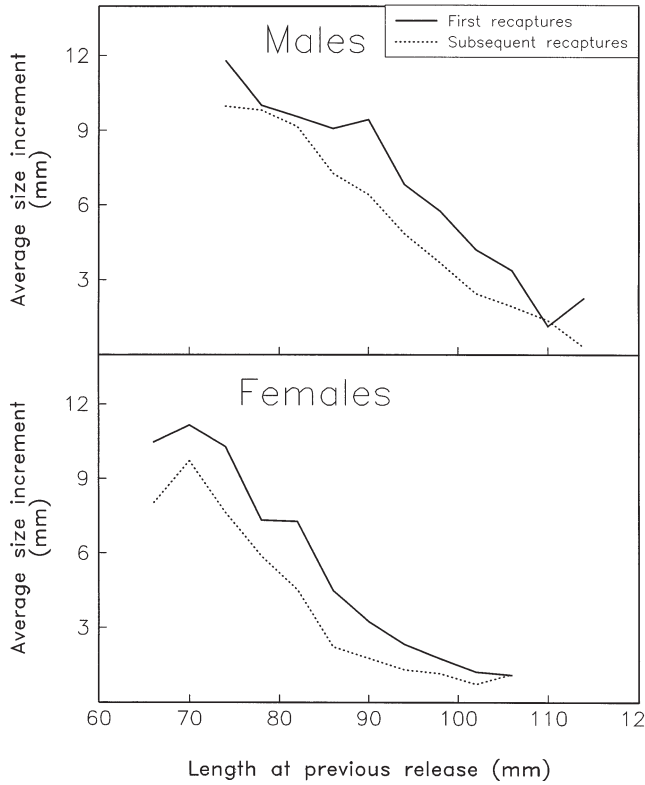
Fig. 2. Mean size increment *v.* size-class for Area 2 by sex. Results are shown for the first recapture of all animals and for subsequent recaptures. Data are provided only for size-classes for which at least 10 recaptures are available.

would be re-released and might be recaptured. On the other hand, if it grew to exceed the minimum size, it would be retained by the fisher. Thus, there is a tendency for multiple recaptures to represent slow-growing individuals. Fig. 2 illustrates this by plotting the mean size increment for first and subsequent recaptures against length at release for Area 2. The results in Fig. 2 are only qualitative because of differences in time of release and time at liberty between the two groups, but they suggest that using the second and subsequent recaptures will lead to bias. The analyses of this paper therefore consider only the first recapture of each animal.

Specifying the size-transition model

The general form for the entries in the size-transition matrix (for a given area, season and sex) is

$$P_{i,j} \propto \int_{\ell^-(i)}^{\ell^+(i)} F[\underline{\phi}, \ell(j), l] \, dl, \qquad (2)$$

where l is length, F is some pre-specified function, $\ell^+(i)$ is the upper limit of size-class i, $\ell^-(i)$ is the lower limit of size-class i, $\ell(j)$ is the average of the upper and lower limits for size-class j, and $\underline{\phi}$ is a vector of parameters.

Eqn 2 implies that growth is a function of the mean of the limits for the size-class. This assumption could be relaxed so that the distribution of lengths within each size-class is taken into account. However, this is ignored here for computational convenience and because the impact of this assumption is unlikely to be substantial. The constant of proportionality in Eqn 2 is chosen so that the constraint $\sum_{i=j}^{x} P_{i,j} = 1$ is satisfied.

Two choices for the function F are considered—normal (for this model, the lower limit for the integral in Eqn 2 is taken to be $-\infty$ when the value of $P_{i,i}$ is being computed):

$$F[\underline{\phi}, \ell(j), l] = \frac{1}{\sqrt{2\pi}\sigma} \exp\left(-\frac{[l - \ell(j) - I(\underline{\phi}, j)]^2}{2\sigma^2}\right), \qquad 3(a)$$

and gamma:

$$F[\underline{\phi}, \ell(j), l] = \frac{\exp\{-\gamma[l - \ell(j)]\}[l - \ell(j)]^{r-1}}{\Gamma(r)\gamma^{-r}}, \qquad (3b)$$

where $r = 1/CV^2$ and $\gamma = 1/[I(\underline{\phi}, j)CV^2]$.

The function $I()$ in Eqns 3a and 3b specifies the expected size increment as a function of size-class (the expected size increments for the normal and gamma functions will differ if a quantifiably important proportion of the normal distribution lies below a size increment of 0). Eqn 3a assumes that the standard deviation of the size increment is constant, whereas Eqn 3b assumes that the coefficient of variation (CV) of the size increment is constant. The gamma function is considered in addition to the normal function because it allows for skewness.

For the analyses of this paper, the function $I()$ is taken to be the Schnute growth model (Schnute 1981; Francis 1995). The most general form of this model ($a \neq 0$ and $c \neq 0$) is given by

$$\begin{aligned}
I(\underline{\phi}, i) &= [a\ell(i)^c + b(1 - a)]^{1/c} - \ell(i), \\
a &= (\ell_2^c - \ell_1^c)/(\lambda_2^c - \lambda_1^c), \\
b &= (\lambda_1^c \ell_2^c - \ell_1^c \lambda_2^c)/(\lambda_1^c - \ell_1^c + \ell_2^c - \lambda_2^c),
\end{aligned} \qquad (4)$$

where ℓ_1 and ℓ_2 are two sizes (taken to be 80 mm and 100 mm for the analyses of this paper) and λ_1 and λ_2 are the expected sizes of animals of sizes ℓ_1 and ℓ_2 after growth.

Francis (1995) can be consulted for further information regarding the choice of parameterization and the equations for the special cases of $a = 0$ or $c = 0$. The Schnute growth model is considered because it can capture a variety of commonly used growth models. For example, the choice of $c = 1$ can be shown to correspond to the standard von Bertalanffy growth equation.

Eqns 3 and 4 are insufficiently flexible to capture the information on size increment adequately. In particular, the probability of not growing (i.e. $P_{i,i}$) is generally underestimated (23% of the recaptured males and 35% of the recaptured females grew by less than 2 mm). One way to increase the flexibility of the model is to introduce additional parameters. The approach considered in this paper is

$$P_{i,j} \rightarrow (P_{i,j})^{\gamma_{i-j}} \left/ \sum_{l=j}^{x} (P_{l,j})^{\gamma_{l-j}} \right., \qquad (5)$$

where γ_k is a parameter that modifies the value of $P_{i,j}$, with $k = i - j$. The number of γ_k values to estimate (rather than to fix equal to 1) is selected by examining the fits to the data. Note that the introduction of these parameters implies that $I()$ is no longer the expected size increment for either of the choices for the function F.

The estimable parameters of the model are therefore c, λ_1, λ_2, σ^2 (or CV^2) and the γ_k values.

Parameter estimation

The likelihood function for the simple case in which growth occurs instantaneously at one time during the year and selectivity is independent of size is outlined first. The extensions necessary to incorporate the possibility of size-dependent selectivity and to handle continuous growth, tagging and recapture are given thereafter.

I. Instantaneous growth, uniform selectivity. For this case, it is assumed that all tags are placed immediately before growth and that recovery occurs immediately after growth. The vector $\underline{N}$ is taken to represent the number of tagged animals that are recaptured, by size-class at release (i.e. N_i is the number of recaptures that were in size-class i when they were released). The expected number of animals released in size-class j that were recaptured in size-class i, $\hat{O}_{i,j}$, is therefore given by

$$\hat{O}_{i,j} = P_{i,j}N_j. \tag{6}$$

The likelihood is derived by assuming that the N_j recaptures of animals that were in size-class j when they were released represent a simple random sample from the total number of animals released that were in size-class j. This implies that the recapture process is multinomial, and hence the likelihood function (L) is given, up to a constant independent of the model parameters, by

$$L = \prod_j \prod_{i \geq j} (P_{i,j})^{O_{i,j}}, \tag{7}$$

where $O_{i,j}$ is the observed number of animals released in size-class j and recaptured in size-class i.

II. Instantaneous growth, non-uniform and known selectivity. If the probability of recapture as a function of the size-class at recapture is known, the likelihood function (Eqn 7) is extended to

$$L = \prod_j \prod_{i \geq j} (p_i P_{i,j} / \sum_{k \geq j} p_k P_{k,j})^{O_{i,j}}, \tag{8}$$

where p_i is the (relative) probability of capturing an animal in size-class i (the selectivity associated with an individual in size-class i).

Apart from consideration of uniform selectivity (in which case, Eqn 8 collapses to Eqn 7), the possibilities that selectivity follows a logistic curve or a gamma function are considered. Bergh and Johnston (1992) assume that selectivity has the logistic form, whereas Sullivan *et al.* (1990) assume that selectivity follows the gamma function.

All three of these selectivity functions might be plausible *a priori* for rock lobster. The assumption that selectivity is uniform arises from the hypothesis that once an animal has been captured it becomes fully vulnerable to the gear. Under this assumption, the population has one component containing those animals that have never been captured and for which the probability of capture depends on size, and another component containing those animals that have been captured at least once and that now all have the same probability of recapture. The assumption of logistic selectivity is based on the hypothesis that larger animals are more vulnerable to capture than are smaller animals. The assumption that selectivity follows a gamma function arises from either the hypothesis that there is an optimal size of capture or the hypothesis that the larger animals tend to migrate from the region of exploitation and are hence less likely to be recaptured.

III. Instantaneous growth, estimated selectivity. If the selectivity pattern is unknown, it can be estimated from the tagging data by noting that the recaptures can be assumed to be a multinomial sample from the releases, with the probability of recapturing an animal in size-class i being proportional to the product of the number that are in size-class i at the time of recapture, $\sum_{j \geq i} P_{i,j}R_j$, where R_j is the number of animals released in size-class j, and the selectivity for that size-class, p_i. The likelihood function therefore includes two contributions. The first is given by Eqn 8, as before, and the second by

$$L = \prod_i (p_i \sum_{j \leq i} P_{i,j}R_j / \sum_k p_k \sum_{i \leq k} P_{k,l}R_l)^{Z_i}, \tag{9}$$

where Z_i is the number of animals recaptured in size-class i.

IV. Continuous growth, tagging and recapture. The case in which tagging and recapture occur throughout the year and growth is not instantaneous is dealt with by dividing the year into several discrete periods and estimating size-transition matrices for each of these periods. For the analyses in this paper, four periods are considered: January–March, April–June, July–September and October–December (Periods 1–4 respectively). It is assumed that growth occurs instantaneously at the end of each period. This assumption is undoubtedly violated but is necessary to reduce the many estimable parameters to a manageable number. Also, the size-based model used to assess the resource operates with a monthly time-step, so allowing growth to occur every three months seems adequate.

Denoting the size-transition matrix for Period q by $\mathbf{P}_q$, the expected size distribution of N_i animals initially in size-class i, released in Period 1 and recaptured during Period 3, $(\hat{O}_{i,j})^{1-2}$, is given by

$$(\hat{O}_{i,j})^{1-2} = \mathbf{P}_2 \mathbf{P}_1 N_j = (P_{i,j})^{1-2} N_j, \tag{10}$$

where $(P_{i,j})^{1-2}$ denotes the i,jth entry in the matrix constructed by multiplying $\mathbf{P}_2$ by $\mathbf{P}_1$.

The contribution to the likelihood function by recaptures that were released in Period 1 and recaptured during Period 3 is therefore

$$L = \prod_j \prod_{i \geq j} [(P_{i,j})^{1-2}]^{(O_{i,j})^{1-2}}. \tag{11}$$

The full likelihood is obtained by combining contributions to the likelihood function for all combinations of period of release and time at liberty (in periods). To simplify the calculations, the time at liberty is restricted to two years. This restriction excludes only a handful of data points except for Area 5.

If selectivity is assumed to be non-uniform and known, Eqn 11 is extended along the lines of Eqn 8, whereas if selectivity is estimated, it is also necessary to include Eqn 9 in the likelihood. For the analyses of this paper, values for parameters c, λ_1, λ_2, σ^2 and $\{\gamma_j: j = 0, 1, 2, \ldots\}$ are estimated separately for each of the four periods.

Model selection and variance estimation

The specifications above define a large number of potential growth models with an associated large number of parameters. The estimates of these parameters are obtained by the simplex method (e.g. Press *et al.* 1988). The models described above are all highly non-linear and so estimating their parameters is time-consuming. It is computationally impossible to consider every possible model for all of the data sets. Instead, various models are applied to the data for Area 2 (Fig. 1) and a 'best' model is selected by the likelihood ratio test (Mood *et al.* 1974).

The variance estimates are obtained by an asymptotic method (Draper and Smith 1966). These estimates should be viewed with some circumspection because the negative log-likelihood is non-quadratic. In principle, more reliable estimates of variance might be obtained by a bootstrap approach (Efron 1982). Unfortunately, this approach is too demanding computationally to be implemented for this model.

Results and discussion

The analyses of this paper are all based on Approach IV (continuous growth, tagging and recapture). For all but one of the analyses, the selectivity contribution (Eqn 9) is included in the likelihood that is maximized to estimate the values for the model parameters.

Model selection

Table 2 lists the negative of the logarithm of the likelihood function for different values of k (the number of

Table 2.   Negative of the logarithm of the likelihood function (ignoring constants) for fits to the data for Area 2

Results are shown for models in which the value of the parameter c is estimated and in which it is fixed equal to 1. Results for the case $c = 1$ are shown for the logistic and uniform selectivity functions

| k | Males | | | Females | | |
| | c estimated | $c = 1$ | | c estimated | $c = 1$ | |
	Logistic	Logistic	Uniform	Logistic	Logistic	Uniform
0	1243·46	1252·46	1435·91	908·49	925·91	941·44
1	1197·59	1203·99	1434·34	904·73	913·57	937·62
2	1195·29	1201·44	1326·88	881·21	889·52	931·85
3	1163·57	1165·33	1226·39	879·42	880·70	923·83
4	1145·28	1145·90	1194·48	875·63	877·22	884·97
5	1139·63	1142·46	1188·60	873·67	875·39	882·21
6	1137·47	1139·23	1151·06	871·71	873·21	879·57
7	1137·32	1137·59	1147·30	870·05	870·06	875·88
8	1137·06	1137·24	1144·88	866·61	868·77	874·54

Table 3.   Selected value for k (the number of values of γ to estimate) for each of the eight data sets

Area	Males	Females
1	1	2
2	4	3
5	8	8
8	3	2

γ parameters for each period; see Eqn 5) for Area 2. Results are shown separately for males and females and for models that fix the growth equation parameter c equal to 1 and that treat c as a free parameter to be estimated along with the other model parameters. Table 2 also provides results for the logistic and uniform selectivity functions in the case $c = 1$. As expected, the negative log-likelihood decreases with an increase in the value of k and if c is estimated. For values of $k < 3$, the model that estimates c is statistically superior to that which fixes $c = 1$ (at the 5% level). However, for values of $k \geq 3$, the model with $c = 1$ is not significantly poorer than the model with c estimated. The best choices for k are 4 (males) and 3 (females) on the basis of the likelihood ratio test. For these values of k, the assumption $c = 1$ appears justified. The reason that the $c = 1$ model provides an adequate fit to the data if $k \geq 3$ is that the flexibility provided by estimating c is more than compensated for by estimating the γ_k values. No attempt is made to select values of k separately for each of the four periods because of computational restrictions. Undoubtedly, fewer parameters would have been needed and hence confidence intervals would have been tighter if this had been possible. For the same reason, no attempt is made to test whether parameter values are the same among areas (Cruywagen 1997).

The logistic selectivity function provides a markedly better fit to the data than either the assumption of uniform selectivity or that of gamma selectivity (Table 2). The normal function (Eqn 3a) provides a much better fit than that of the gamma function. Bergh and Johnston (1992) base their analyses on a beta distribution function. Preliminary analyses with this function indicate that the normal function is superior. The remaining calculations of this paper are therefore based on models that fix $c = 1$, assume the normal function, and incorporate a logistic selectivity function.

Table 3 lists the values for k for each of the eight data sets (two sexes times four areas). There is strong agreement

between the growth rate and the number of estimated parameters—the most parameters are estimated for each sex in Area 5.

The fit of the model to the data for Area 2 is summarized in Fig. 3 by three plots for each sex. The top plots in Fig. 3 show the observed and model-predicted length–frequency distributions for the recaptured animals, the middle plots show the observed and model-predicted size increments, and the bottom plots show the observed and model-predicted length–frequency distributions for the lengths of the recaptured animals when they were released. The model estimate of the probability of recapturing an animal released during Period 1 and at liberty for one period is computed as

$$\sum_i p_i P_{i,j} R_j \Big/ \sum_{j'} \sum_{i'} p_{i'} P_{i',j'} R_{j'}. \tag{12}$$

For ease of presentation, the results in each plot in Fig. 3 are summaries across time at liberty and month of release (and length at release for the middle plots). The top and middle plots can be used to examine the quality of the fit to the growth information, and the bottom plots can be used to assess whether selectivity has been modelled adequately. None of the plots in Fig. 3 suggest model mis-specification, which indicates that the model provides an adequate fit to the available data.

Fig. 4 shows plots of observed and predicted distributions for size increment, the most important output of the model, for Areas 1, 5 and 8. There is no evidence for model mis-specification in Fig. 4.

Estimates of growth

Plots of mean size increment at the end of each of the four periods (March, June, September and December) against length are shown for Area 2 in Fig. 5, and Fig. 6 provides means and 90% confidence intervals for annual size increment against length for that area. Fig. 7 plots the point estimates of the annual size increment against length for all four areas.

Care needs to be taken in interpreting the within-year growth patterns because the model incorporates only four possible occasions at which growth can occur. Thus, if growth actually occurs at the end of October, the growth of
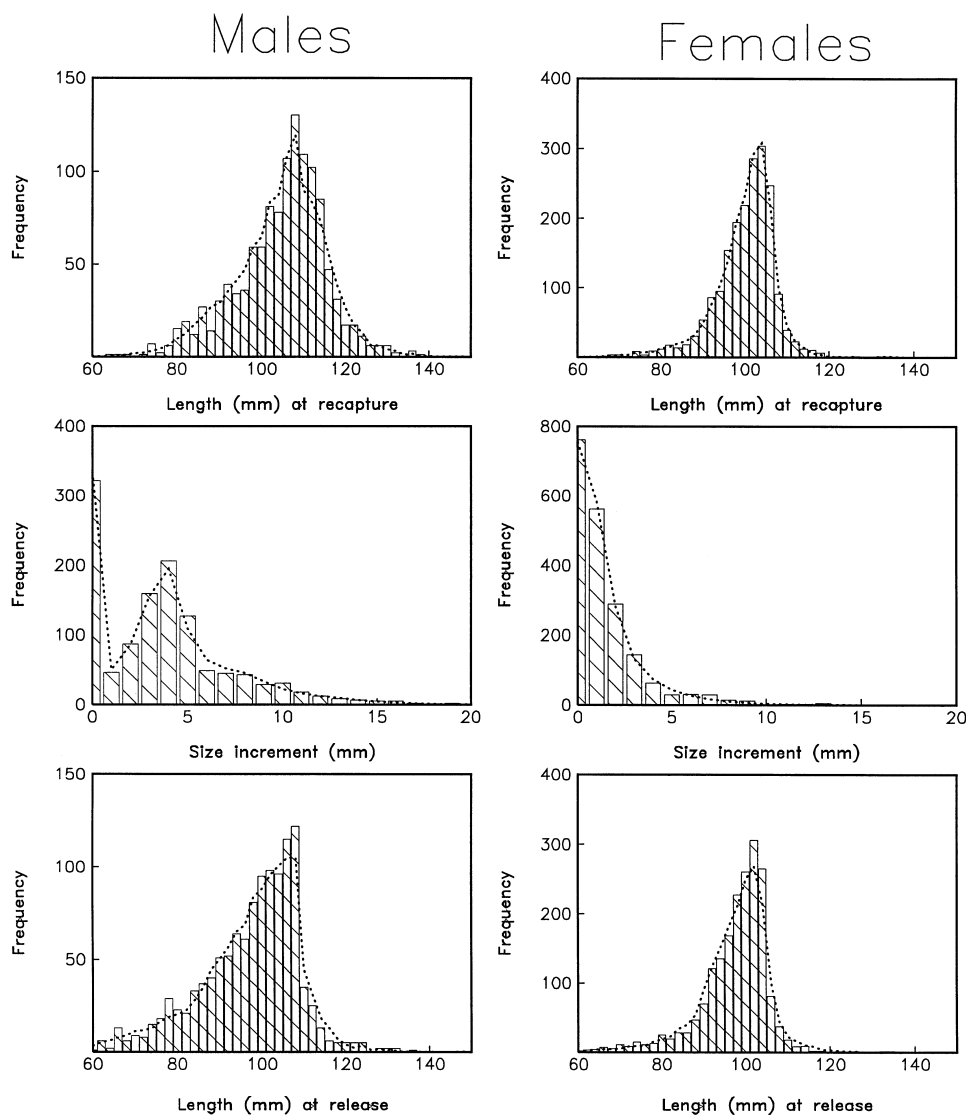
Fig. 3. Diagnostic plots for Area 2. Results are presented separately for males and females. The plots represent summaries across time at liberty and month of release (and length at release for the middle plots). The bars represent the observed data and the dotted lines the model predictions.

animals released in October and recaptured in January will be reflected as growth that occurred at the end of December, whereas the growth of animals released in September and recaptured in December will be reflected as growth that occurred at the end of September. If growth occurred at the same time for all animals, this problem could be overcome by dividing the year appropriately. However, this is not the case in reality (and in any case there is likely to be some interannual variation in the timing of moulting).

Bearing the above caveats in mind, for males in Area 2 there appears to be little growth at the end of June, whereas the end of September appears to be the time at which most of the legal-size ($\geq$110 mm CL) animals grow. Some growth of males is estimated to take place at the end of December and at the end of March, but this is restricted primarily to

sub-legal animals. The growth pattern for females in Area 2 is notably different from this, with much lower growth rates and peaks in growth for legal-size ($\geq$105 mm CL) females in March and June. The growth patterns for sub-legal females in December and June are similar to each other, as are those in March and September for these females.

The nearly constant mean size increment for males in Area 2 at the end of September (Fig. 5) indicates that the decline in annual size increment for these animals (Fig. 6) is caused by a reduction in the mean size increment at other times of the year (probably an artefact of reduced moulting frequency). September–October is the primary moulting period for legal-size males in Area 2 (e.g. Frusher *et al.* 1997), so any reduction in moulting frequency is likely to arise from the cessation of moulting at other times of the year. Annala
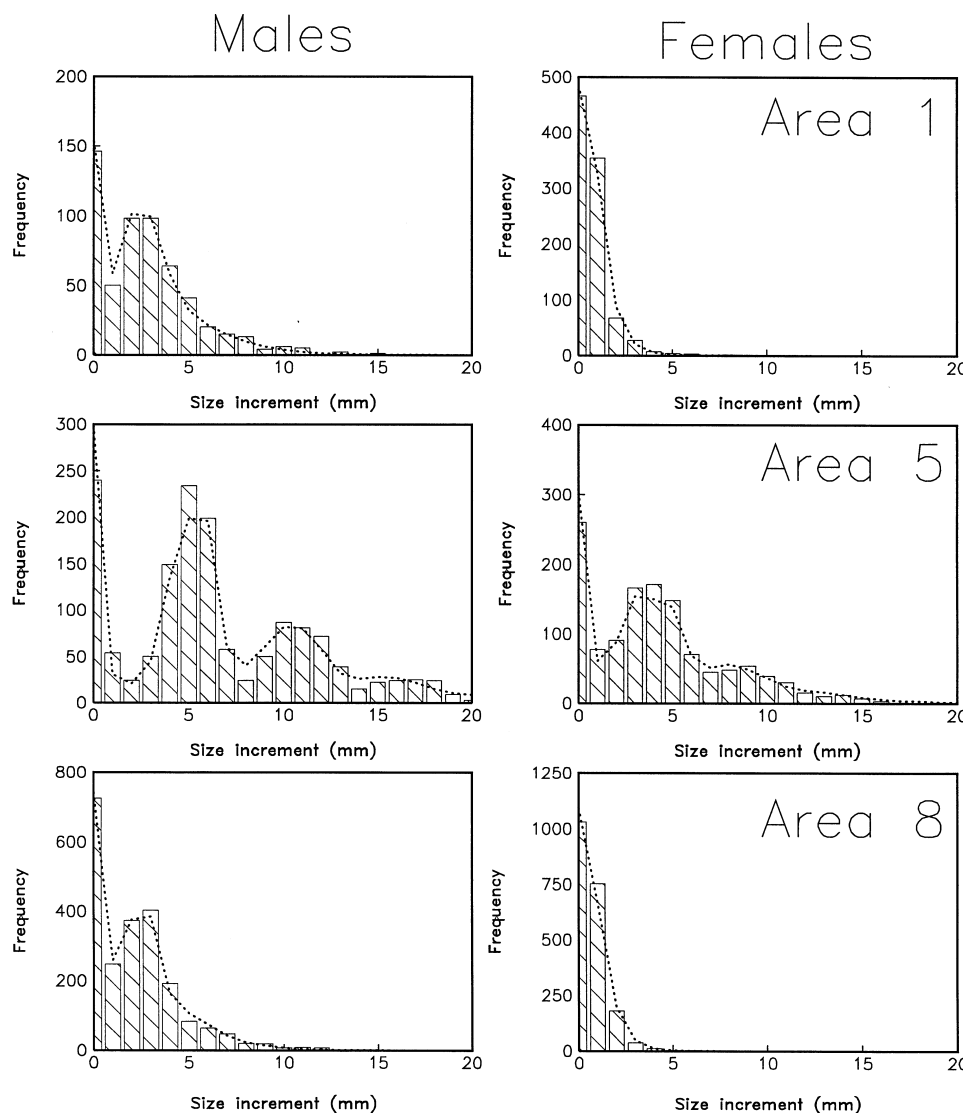
Fig. 4. Observed and model-predicted distributions of size increment for Areas 1, 5 and 8. The plots represent summaries across length at release, time at liberty and month of release. The bars represent the observed data and the dotted lines the model predictions.

and Bycroft (1988) found no relationship between growth per moult and size for male *J. edwardsii* in New Zealand but did find significant relationships between (declining) moulting frequency and annual size increment with increasing size.

The annual size increments for females in Area 2 (Fig. 6) are far more precise than those for males. The annual size increment for 60-mm males is very similar to that for 60-mm females, but the male growth rate is higher for larger sizes.

Kennedy and Tarbath (1992) showed that the growth rates of lobsters decrease from the north to the south of Tasmania and that, in each region, males grow faster than females. This is supported by the results of the present analysis (Fig. 7). The result for females in Area 8 appears anomalous because the annual size increment is essentially constant

over all lengths. Females in Area 8 are known to grow slowly (Fig. 4) and size increments of 1 mm (and perhaps less) are possible. The restriction of the analysis to 2-mm size-classes may have led to the result in Fig. 7 for Area 8. This is perhaps not of much concern from a management perspective because females in Areas 1 and 8 rarely reach the minimum legal size of 105 mm CL (Frusher *et al.* 1997) and hence the possibility of overexploitation is slight if the impact of discarding is small.
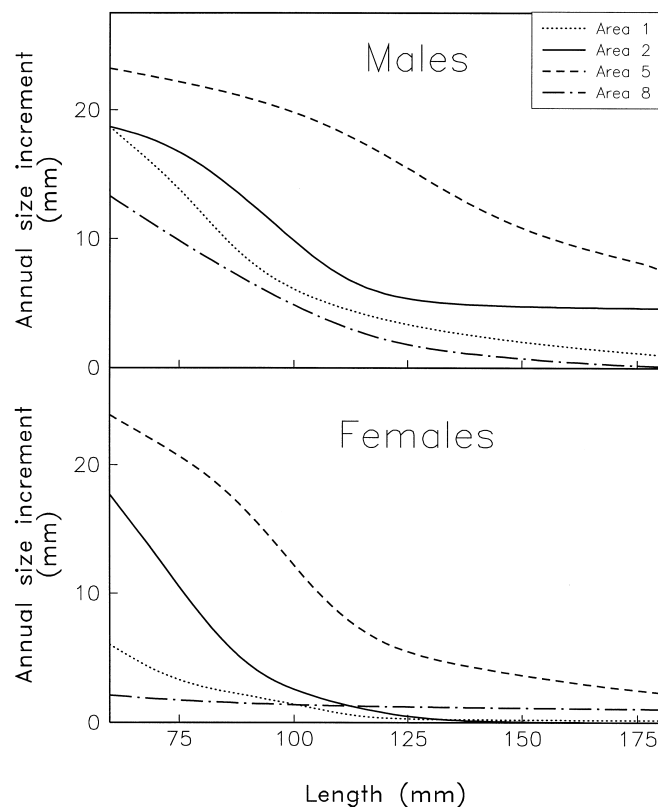
Size-specific selectivity

Fig. 8 shows the estimated selectivity curves. For all but Area 2, the selectivity of females is estimated to be higher than that of males for lengths of >75 mm and selectivity for a
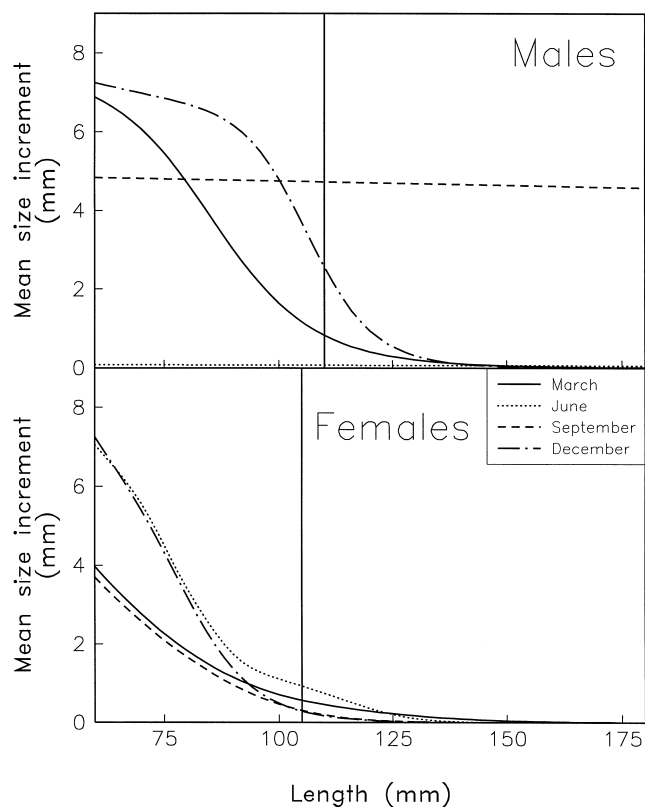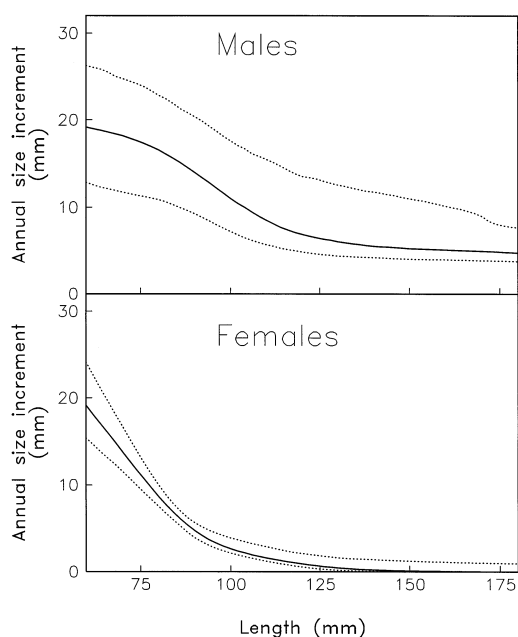
Fig. 5. Estimates of mean size increment against length for animals in Area 2. The vertical lines indicate the current minimum legal sizes.

Fig. 7. Annual size increment against length for Areas 1, 2, 5 and 8.

Fig. 6. Means and 90% confidence intervals for the annual size increment against length for Area 2.

length of 60 mm is close to 0. In contrast, the selectivity curve for Area 2 is flatter, with the selectivity of males exceeding that of females for all lengths. The reason for the difference between the selectivity pattern for Area 2 and those for the other areas is currently unknown but may be a function of differences in the behaviour of animals among areas, differences in reporting rates of undersized animals by fishers among areas, and differences in fraction of the catch taken with scientific and commercial gears. The scientific gear does not include escape gaps and so should have a more constant selectivity pattern than that of the commercial gear—the estimates of selectivity presented in Fig. 8 are averages of those for the commercial and scientific gears, with the relative contribution to the average presumably depending on the fraction of animals recaptured with each type of gear.

Fig. 9 shows estimates of annual size increment against length for Area 2 from an analysis that ignores the contribution to the likelihood for the length-at-release data (Eqn 11) and assumes uniform selectivity. These results are more optimistic than those in Fig. 7 (reproduced as 'base-case' in Fig. 9). The impact of ignoring selectivity is most marked for females, because selectivity is estimated to be more strongly dependent on length for females (Fig. 8). It is therefore necessary to attempt to account for selectivity
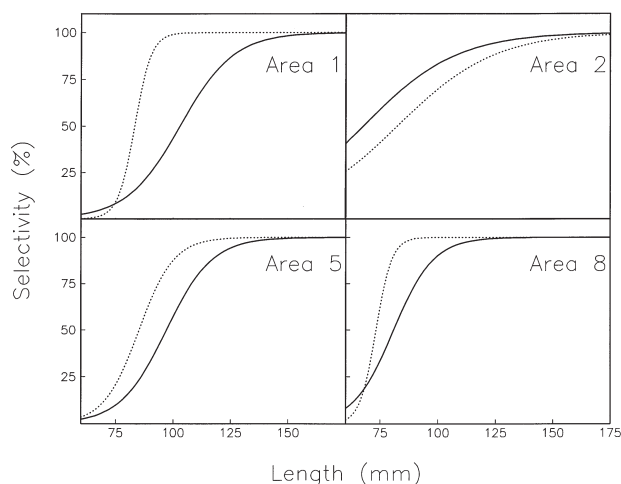
Fig. 8. Model-estimates of size-specific selectivity. Results are presented for (—) males and (- - - -) females for each of Areas 1, 2, 5 and 8.
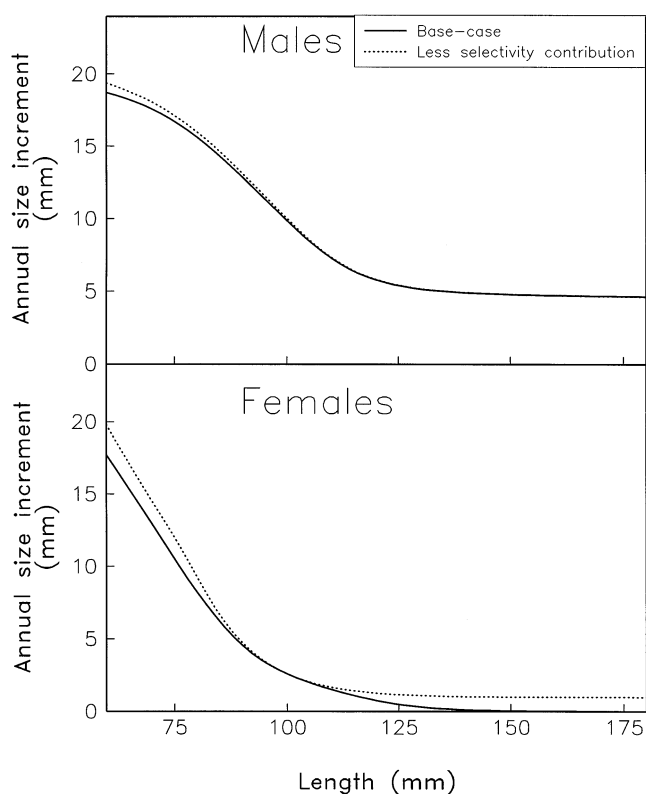

Fig. 9. Estimates of annual size increment against length for Area 2 based on the base-case analysis and on an analysis that ignores the contribution of selectivity to the likelihood function and assumes uniform selectivity.

when analysing tag–recapture data. The selectivity curves for Areas 1, 5 and 8 are estimated to be more steep than that for Area 2 (Fig. 8). It therefore seems likely that the impact of ignoring selectivity for these areas would be more severe than is the case for Area 2.

Equilibrium length distributions

Johnston and Bergh (1993) used estimates of length distributions at unexploited equilibrium, $\underline{N}$, determined from their size-transition matrix along with length distributions for unexploited stocks, to estimate natural mortality rates for *J. lalandii* off South Africa. The calculation of this distribution involves solving the following equation for $\underline{N}$:

$$\underline{N} = \mathbf{MP}\underline{N} + \underline{R}, \tag{13}$$

where $\mathbf{M}$ is a diagonal matrix with non-zero elements equal to e^{-M}, M is the instantaneous rate of natural mortality, and $\underline{R}$ is the vector of settling animals.

Settlement of pueruli is assumed to be occur at a length of 10 mm, so

$$R_l = \begin{cases} 1 & \text{if } l = 10 \text{ mm,} \\ 0 & \text{otherwise.} \end{cases} \tag{14}$$

In order to apply Eqn 13, it is necessary to specify entries in the size-transition matrix for all lengths between 10 mm and the largest length considered (240 mm). The growth rate for animals smaller than 60 mm is assumed to be same as that for 60-mm animals. For Area 2, this assumption implies an annual size increment for pueruli of roughly 19 mm CL (Fig. 7). This size increment is consistent with the observations that juveniles of *J. edwardsii* in Gisborne, New Zealand, grew to about 38 mm in one year (McKoy and Esterman 1981), juveniles of *J. novaehollandii* reached a mean size of 36·5 mm CL one year after settlement (pueruli, 10·3 mm) (Lewis 1977), and juveniles of *J. lalandii* reached 22–24 mm CL one year after settlement (pueruli, about 10 mm) (Pollock 1973).

Fig. 10 shows length distributions at unexploited equilibrium for Areas 1, 2 and 5 for the assumption $M = 0·1 \text{ year}^{-1}$. The assumption that M is independent of size is undoubtedly incorrect because M is larger than $0·1 \text{ year}^{-1}$ for the smaller animals. However, this is unlikely to affect the results for the size range in Fig. 10. The mode of the length distribution in Fig. 10 decreases as one moves from north (Area 5) to south (Area 1). Males in Areas 2 and 5 are estimated to grow into the largest size-class considered in the model, 240 mm. The impact of changing the value assumed for M is illustrated in Fig. 11 for Area 2. At lower values for M, the mode of the length distribution occurs at a larger size and a greater fraction of the population is in the 240-mm size-class.
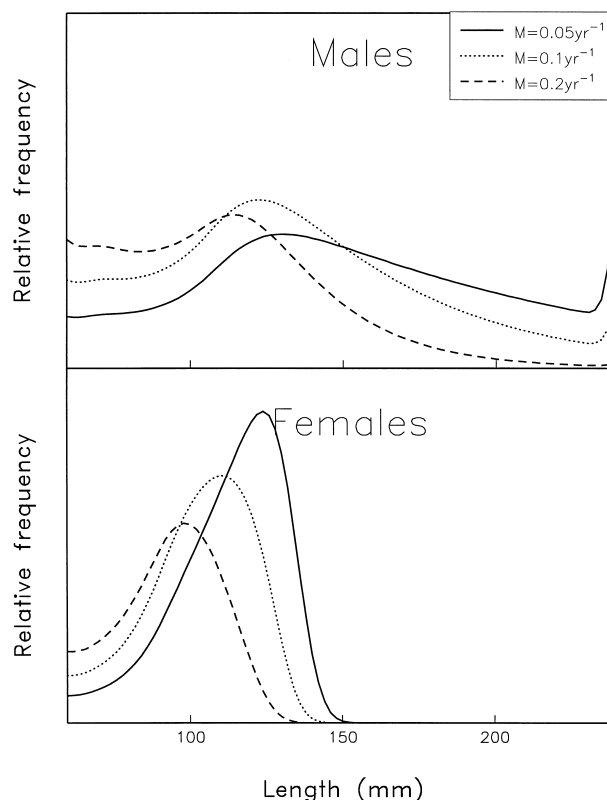
General discussion

The method applied in this paper is designed specifically to be used for assessments based on a size-transition matrix. The use of a size-transition matrix to model growth accounts to some extent for variability in growth among individuals.
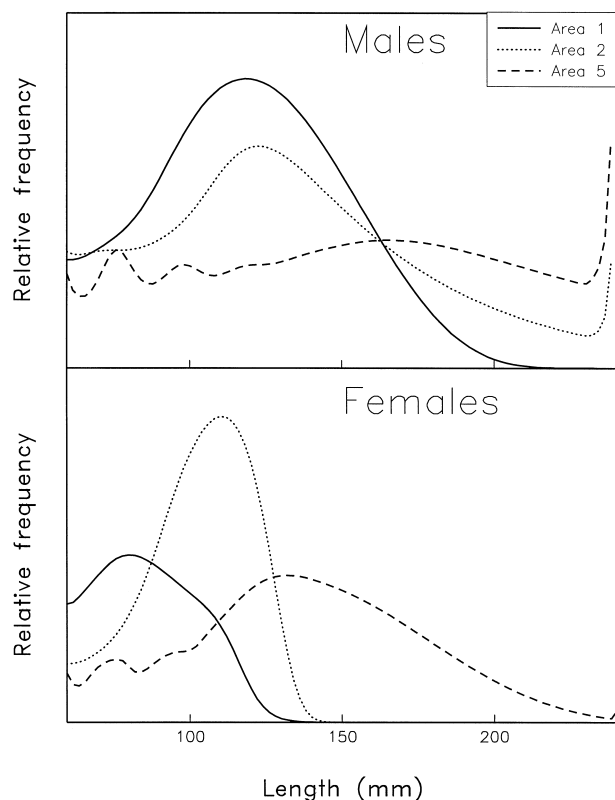
Fig. 10. Length distributions for lobster populations in Areas 1, 2 and 5 at unexploited equilibrium. The calculations in this figure assume an (age-independent) rate of natural mortality of 0.1 year^{-1}.

Fig. 11. Length distributions at unexploited equilibrium for Area 2. Results are shown for three alternative choices for the instantaneous rate of natural mortality, *M*.

Such variability is known to bias conventional methods for estimating growth rates from tag–recapture data (Sainsbury 1980; Maller and deBoer 1988; Wang *et al.* 1995). One criticism of the size-transition matrix approach is that it assumes that the growth pattern is a function of size alone, when in reality the expected size increment of a group of animals might also be a function of age. Deriso and Parma (1988) consider a model that incorporates the effects of both age and size. One problem related to the lack of age-dependence in the size-transition matrix is that animals are all predicted to grow eventually into the largest size-class considered in the model, whereas in reality each animal has its own maximum size. Although this problem clearly needs to be addressed in future work, it is currently not of major consideration for Tasmanian rock lobster because the incorporation of natural mortality in the population dynamics model used for assessment purposes ensures that animals do not live forever. More importantly, however, this problem will be most severe if attempts are made to extrapolate the population biomass beyond the range of historical experience, whereas current management strategies for this resource are designed to keep the biomass within this range.

The results of this study are undoubtedly affected by a variety of biases. The most important of these is probably the restriction of the analysis to 2-mm size-classes to reduce the impact of measurement error. Although this should not affect the results for animals in Areas 2 and 5 and for males in Areas 1 and 8 substantially (because growth in these areas is fast), the results for females in Areas 1 and 8 may be biased to some extent. Another potential source of bias is that fishers may return undersized lobsters to the sea without reporting tags. A more serious source of bias is fishers not reporting recaptures of legal-size animals, as returned undersized lobsters are available for capture and reporting later. This will lead to negative bias in growth rates.

An assumption that is fundamental to this method is that growth for tagged and untagged animals does not differ substantially. Growth rates derived from tagged animals may differ from those for untagged animals because of the effects of confinement, exposure to air and injuries caused by handling. Although this assumption is virtually impossible to validate, McKoy and Esterman (1981) suggest that it is valid for *J. edwardsii* in New Zealand. Chittleborough (1974) shows that the loss of two limbs did not affect the mean size increment per moult in *Panulirus*

longipes. However, Brown and Caputi (1985) show that exposure to air reduces the moult increment for *P. cygnus.* A further concern is that the scientific component of the present sampling process was non-random with respect to time. Finally, the estimates of selectivity are biased as indicators of the selectivity of commercial fishers to some extent because the gear used by scientists to recapture lobsters does not include escape gaps.

The method applied in this paper differs from the methods for using tag–recapture data to estimate growth rates that are extensions of the approach described by Fabens (1965) because account is taken of the discrete nature of growth and animals are not permitted to 'shrink' following a moult. Unlike in Baker *et al.* (1991), the error structures considered in this paper and by Francis (1995) assume that differences between observations and model predictions are caused by individual variability rather than measurement error. The method differs from those developed specifically for invertebrates (e.g. Fogarty and Idoine 1988) because a more general growth model is considered and because the data are analysed seasonally rather than annually. The method also differs from previous methods by explicitly allowing for the effect of non-uniform selectivity.

The modelling approach considered in this paper allows the analyst to estimate growth rates directly from tag–recapture data. The method currently considers the contributions of the size increment and the distribution of recaptures separately (Eqns 11 and 9). In principle, the method could be extended to combine these two contributions into a single contribution to the likelihood. Such an approach would involve using the model to predict the length distribution of recaptures directly from the length distribution of releases and the time at liberty (by using, for example, an extension of the method of Hilborn 1990, which is based on a Poisson likelihood function). The current approach develops the likelihood function by conditioning on the total number of recaptures given the period of release and time at liberty. This is equivalent to an analysis in which fishing mortality is treated as a nuisance parameter so that the model-predicted number of recaptures equals the observed number. It can be shown that in this case the Poisson likelihood is equivalent to the multinomial likelihood used in this paper.

A further possible extension would be to include the likelihood considered in this analysis in the likelihood that is maximized when the assessment is conducted. Although this approach has several advantages, such as that the posterior distributions used for risk analysis would include the uncertainty about the growth rate information, it is currently computationally impossible to conduct an analysis of this level of complexity.

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