A novel tag-recovery model with two size classes for estimating fishing and natural mortality, with implications for the southern rock lobster (*Jasus edwardsii*) in Tasmania, Australia

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Multi-year tag-recovery models can be used to derive estimates of age- and year-specific annual survival rates and year-specific instantaneous fishing and natural mortality rates. The latter, which are often of interest to fisheries managers, usually can only be estimated when the tag-reporting rate (λ) and the short-term tag-induced mortality and tag-shedding rate (ϕ) are known *a priori*. We present a new multi-year tagging model that permits estimation of instantaneous mortality rates independently of $\phi\lambda$, provided tagged animals from two adjacent size groups are released simultaneously. If the two size groups comprise animals just above and below the minimum harvestable size limit, then it is possible to estimate year-specific instantaneous fishing and natural mortality rates after 2 yr of tagging and tag-recovery. In addition to the standard assumptions of multi-year tag-recovery models, it is necessary to assume that recruited animals have equal selectivity, pre-recruited animals become fully recruited in 1 or 2 yr, and the size groups experience the same natural mortality rate. Applicability of the model to the Tasmania southern rock lobster (*Jasus edwardsii*) fishery is evaluated using a simulation model and parameters based on data from the lobster fishery; assumptions are likely to be met and precision should be adequate if at least 1000 animals are tagged per year in each size group.

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Introduction

The models developed by Brownie *et al.* (1985) form the basis of many modern approaches to estimating mortality rates of exploited populations from tag-recovery data. The models are designed for situations where cohorts of tagged animals are released at known intervals, generally a year apart. If all tagged animals are fully vulnerable to harvesting at the time of release, then the ratio of tag-recoveries from two cohorts released a year apart reflects the fact that the first cohort has experienced one more year of mortality than the second cohort. Consequently, this ratio can be used to derive an estimate of the finite annual survival rate. This class of models can also be parameterized in terms of age-dependent finite annual survival and tag-recovery rates. Suppose a cohort of 5-yr-old animals is released in the first year of a tagging

study and a similar cohort of 6-yr-old animals is released in the second year. During the first year, the 5-yr-old cohort will experience 1 yr of mortality and become age 6. In the second year of the study, both cohorts will be age 6 and should experience the same exploitation rate. As a result, the ratio of tag-recoveries from the two cohorts can be used to estimate the survival rate of the 5-yr-old cohort in the first year.

Generally, only information on the total mortality rate can be obtained from the Brownie *et al.* (1985) models; separation of mortality into its fishing and natural components is theoretically possible but not reliable unless massive amounts of tag-recoveries have been obtained (Youngs, 1974; Hoenig *et al.*, 1998). Pollock *et al.* (1991) showed that if information is available about the tag-reporting rate, then it is feasible to estimate the individual components of mortality. Hoenig *et al.* (1998) utilized the

work by Pollock *et al.* (1991) to reparameterize the Brownie *et al.* (1985) models in terms of instantaneous mortality rates and tag-reporting rate. Although the Hoenig *et al.* (1998) models can be used to estimate natural and year-specific fishing mortality rates directly from tag-recovery data, external information on the tag-reporting rate is generally required to get reliable estimates.

This apparent rule that the tag-reporting rate must be known (and typically known precisely) to calculate estimates of fishing and natural mortality has often plagued practical applications of multi-year tag-recovery models (Latour *et al.*, 2001a). However, Hearn *et al.* (1998) developed an important exception to this rule by showing that it is possible to design a tag-recovery study where the components of mortality can be estimated from a generalized Brownie *et al.* (1985) model without external information on tag-reporting rate. Their approach involves tagging before and after the fishing season so that natural mortality can be measured between fishing seasons. Under this design, the difference between total mortality (which can be derived from Brownie *et al.*, 1985) and natural mortality provides the estimate of fishing mortality.

In this paper, we draw on the theory associated with the age-structured version of the Brownie *et al.* (1985) models and the models developed by Hearn *et al.* (1998) and Hoenig *et al.* (1998) to develop a new model to infer mortality rates when tagged animals from two adjacent size groups are released simultaneously. If the two size groups comprise animals just above and below the minimum harvestable size limit, then it is possible to estimate year-specific instantaneous fishing and natural mortality rates independently of the tag-reporting rate after 2 yr of tagging and tag-recovery. In addition to the standard assumptions of multi-year tag-recovery models (see Pollock *et al.*, 1991, 2001; Latour *et al.*, 2001b for detailed discussions of these assumptions), it is necessary to assume that all recruited animals have equal selectivity, the pre-recruited contingent of the tagged population grows to become fully recruited in 1 yr (this assumption is relaxed in the Appendix), that they experience no fishing mortality during that first year, and that the two size groups experience the same natural mortality rate and tag-reporting rate. Consequently, this model may be most appropriate for a crustacean fishery in

which growth of the sublegal animals to legal size is by a discrete growth pulse such as a molt that occurs between fishing seasons. As such, we present the model in the context of the Tasmania southern rock lobster (*Jasus edwardsii*) fishery since it largely meets these assumptions.

Methods

Development of the model

The structure of the model in its most general form is based on three types of parameters: year-specific instantaneous fishing mortality rates, year-specific instantaneous natural mortality rates, and year-specific tag-recovery rates. As with all tag-recovery models, it is possible to impose restrictions on the parameters to ultimately obtain a more parsimonious model (e.g. assume natural mortality is constant over time). As described above, two size groups of animals must be tagged within the same year under the assumption that the pre-recruited animals are within one annual molt of reaching the minimum legal size limit. To develop the model, let r_{ijp} and r_{ijr} denote the number of pre-recruited and fully recruited animals, respectively, tagged in year i that are recovered in year j. The matrix of tag-recoveries, R, for a study with I yr of tagging and J yr of tag-recovery (J ≥ I) takes the form

$$R = \begin{bmatrix} r_{11r} & r_{12r} & r_{13r} & \cdots & r_{1Jr} \\ 0 & r_{12p} & r_{13p} & \cdots & r_{1Jp} \\ - & r_{22r} & r_{23r} & \cdots & r_{2Jr} \\ - & 0 & r_{23p} & \cdots & r_{2Jp} \\ \vdots & \vdots & \vdots & \ddots & \vdots \\ - & - & - & \cdots & r_{IJr} \\ - & - & - & \cdots & x_p \end{bmatrix}, \qquad (1)$$

where

$$x_p = \begin{cases} 0 & \text{if } I = J, \\ r_{IJp} & \text{otherwise.} \end{cases}$$

Application of multi-year tag-recovery models generally involves constructing a matrix of expected values and comparing them to the observed data. The same approach will be needed to derive parameter estimates for this model. The matrix of expected values corresponding to Equation (1) under a time-specific parameterization is

$$E(R) = \begin{bmatrix} N_{1r}f_1 & N_{1r}\,e^{-(F_1+M_1)}f_2 & N_{1r}\,e^{-(F_1+F_2+M_1+M_2)}f_3 & \cdots & N_{1r}\,e^{-\sum_{k=1}^{J-1}(F_k+M_k)}f_J \\ 0 & N_{1p}\,e^{-M_1}f_2 & N_{1p}\,e^{-(F_2+M_1+M_2)}f_3 & \cdots & N_{1p}\,e^{-\sum_{k=2}^{J-1}F_k-\sum_{k=1}^{J-1}M_k}f_J \\ - & N_{2r}f_2 & N_{2r}\,e^{-(F_2+M_2)}f_3 & \cdots & N_{2r}\,e^{-\sum_{k=2}^{J-1}(F_k+M_k)}f_J \\ - & 0 & N_{2p}\,e^{-M_2}f_3 & \cdots & N_{2p}\,e^{-\sum_{k=3}^{J-1}F_k-\sum_{k=2}^{J-1}M_k}f_J \\ \vdots & \vdots & \vdots & \ddots & \vdots \\ - & - & - & \cdots & y_r \\ - & - & - & \cdots & y_p \end{bmatrix}, \qquad (2)$$

where N_{ir} and N_{ip} represent the number of fully and pre-recruited animals, respectively, tagged in year i, F_i is the instantaneous fishing mortality rate in year i for legal-sized animals, M_i the instantaneous natural mortality rate in year i, and f_i is the tag-recovery rate in year i for legal-sized animals. The expected values corresponding to the (I,J,r) and (I,J,p) cells in the matrix are as follows:

$$y_r = \begin{cases} N_{Ir}f_J & \text{if } I = J, \\ N_{Ir}\, e^{-\sum_{k=I}^{J-1}(F_k+M_k)}f_J & \text{otherwise,} \end{cases} \tag{3}$$

and

$$y_p = \begin{cases} 0 & \text{if } I = J, \\ N_{Ip}\, e^{-M_I}f_J & \text{if } J = I + 1, \\ N_{Ip}\, e^{-\sum_{k=I+1}^{J-1} F_k - \sum_{k=I}^{J-1} M_k}f_J & \text{otherwise.} \end{cases} \tag{4}$$

Moment estimators

To illustrate the logical basis for parameter estimation, the following moment estimators are developed for the case where $I = J$. As with the Brownie *et al.* (1985) models, the tag-recovery rates can be estimated by computing simple ratios of the form

$$\hat{f}_j = \frac{r_{jjr}}{N_{jr}}, \qquad (j = 1, \ldots, J), \tag{5}$$

where the $\wedge$ denotes an estimate. To estimate the fishing mortality rate in year i, ratios involving tag-recoveries from recruited and pre-recruited animals that were tagged in year i must be constructed. Specifically, these ratios lead to expressions of the form:

$$\hat{F}_1 = -\log_e\left(\frac{N_{1p}r_{1jr}}{N_{1r}r_{1jp}}\right), \quad (j = 2, \ldots, J),$$

$$\hat{F}_2 = -\log_e\left(\frac{N_{2p}r_{2jr}}{N_{2r}r_{2jp}}\right), \quad (j = 3, \ldots, J),$$

$$\vdots$$

$$\hat{F}_{I-1} = -\log_e\left(\frac{N_{I-1p}r_{I-1Ir}}{N_{I-1r}r_{I-1Ip}}\right). \tag{6}$$

Note that it is possible to obtain a fishing mortality estimate from one tagging event (provided tag-recoveries are tabulated for at least 2 yr) and it is not possible to estimate the fishing mortality rate in the most recent year of tag-recovery unless additional assumptions are made.

To estimate the natural mortality rate in year i, ratios involving tag-recoveries from pre-recruited and recruited animals in years i and i+1, respectively, must be constructed. These ratios, in turn, lead to expressions of the form:

$$\hat{M}_1 = -\log_e\left(\frac{N_{2r}r_{1jp}}{N_{1p}r_{2jr}}\right), \quad (j = 2, \ldots, J),$$

$$\hat{M}_2 = -\log_e\left(\frac{N_{3r}r_{2jp}}{N_{2p}r_{3jr}}\right), \quad (j = 3, \ldots, J),$$

$$\vdots$$

$$\hat{M}_{I-1} = -\log_e\left(\frac{N_{Ir}r_{I-1Ip}}{N_{I-1p}r_{IIr}}\right). \tag{7}$$

It is not possible to estimate the tag-reporting rate, λ directly from the model. However, given year-specific estimates of mortality (which can be obtained directly from the model) and knowledge of the timing of the fishery, it is possible to obtain an estimate of the exploitation rate. Specifically, for either a pulse (Type I) or a continuous (Type II) fishery (Ricker, 1975), the estimated exploitation rate in year i, $\hat{u}_i$, takes the form

$$\hat{u}_i = \begin{cases} 1 - e^{-\hat{F}_i} & \text{for a Type I fishery,} \\ \dfrac{\hat{F}_i}{\hat{F}_i + \hat{M}_i}\left(1 - e^{-(\hat{F}_i + \hat{M}_i)}\right) & \text{for a Type II fishery.} \end{cases} \tag{8}$$

If the exploitation rate estimate is used in combination with the tag-recovery rate estimate (which can also be obtained directly from the model), it is then possible to derive an estimate of the tag-reporting rate. Thus,

$$\hat{\lambda} = \frac{\hat{f}_i}{\hat{\varphi}\hat{u}_i}, \tag{9}$$

where $\hat{\varphi}$ is an estimate, obtained external to the analysis, of the probability that an animal survives any initial tag-shedding and tag-induced mortality (Pollock *et al.*, 1991; Hoenig *et al.*, 1998). If λ and M are assumed to be constants over time, and the timing of the fishery is known, then the tag-recovery rate in the last year of tag-recovery can be used to estimate the fishing mortality rate in that year.

The likelihood function

The method of maximum likelihood is typically used to obtain parameter estimates from multi-year tag-recovery models because it is generally more efficient than applying moment estimators. The method consists of two steps. First, the probability of observing a particular set of tag-recoveries is expressed in terms of the unknown mortality and tag-recovery parameters. The resulting mathematical expression is called the likelihood function. Second, the values of the parameters that maximize the likelihood function are found. Those values, which are the maximum likelihood parameter estimates, yield the highest probability for observing the actual number of tag-recoveries. For the size-structured model presented herein, the quantities r_{ijr} and r_{ijp} simply represent realizations of the random variables R_{ijr} and R_{ijp}, respectively. Although these random

variables are modeled by the expressions in the matrix of Equation (2), for convenience let $E(R_{ijr}) = N_{ijr}P_{ijr}$ and $E(R_{ijp}) = N_{ijp}P_{ijp}$. The tag-recoveries over time from each tagged cohort are assumed to follow a multinomial probability distribution, and if we assume independence among all tagged cohorts, the overall product likelihood takes the form

$$\Lambda \propto \prod_{i=1}^{I} \left(\prod_{j=i}^{J} P_{ijr}^{r_{ijr}} \right) \left(1 - \sum_{j=i}^{J} P_{ijr} \right)^{N_{ir} - \sum_{j=i}^{J} r_{ijr}}$$

$$\times \prod_{i=1}^{I} \left(\prod_{j=i+1}^{J} P_{ijp}^{r_{ijp}} \right) \left(1 - \sum_{j=i+1}^{J} P_{ijp} \right)^{N_{ip} - \sum_{j=i+1}^{J} r_{ijp}} . \quad (10)$$

Maximizing the likelihood in Equation (10) can be accomplished numerically through an iterative process.

Potential application to southern rock lobsters

The southern rock lobster (*J. edwardsii*) is an extremely important natural resource to the island of Tasmania, Australia, with recent landings exceeding A\$50 million in value (Frusher, 2001). However, reports of high exploitation rates generated concern for this fishery. As a result, in 1992 the Tasmania Aquaculture and Fisheries Institute (formerly the Department of Primary Industry and Fisheries) commenced a fishery independent catch sampling project to provide fishery assessment parameters. Results from this project and the mandatory catch and effort logbook data from the commercial fishery form the basis of annual stock assessments of the fishery.

The overall stock assessment is based on fitting a population dynamics model to rock lobster data from each of eight defined zones around Tasmania (Punt and Kennedy, 1997). These eight areas are assessed separately because of significant spatial variation in growth rates, size at maturity, and catch rates. Incorporated within the model are area-specific descriptions of lobster growth, size-specific maturity rates, length-specific fecundity, and an estimate of the natural mortality. Growth rates are one of the most important inputs to the model and fortunately, in recent years, scientists in Tasmania have been conducting a large-scale tagging study on rock lobsters to obtain such information.

Southern rock lobster life history and fishery considerations

Here we outline the salient features of southern rock lobster life history and the associated fishery, as they pertain to the application of the two-size category model. Inherent to the model formulation is the assumption that lobsters do not undertake skip molting. To date, scientists working with rock lobsters in Tasmania have never observed an incidence of skip molting. In general, molting frequency and growth of rock lobsters varies regionally. Off southern Tasmania, lobsters molt once per year over a wide range of sizes

including the sizes in the commercial catch, while off northern Tasmania, animals molt twice per year and tend to experience higher annual growth increments. Although rock lobster growth is variable, it has been characterized rather well. Lobsters tend not to feed at the time of molting and tagging data suggest that rock lobsters undergo limited movements (Pearn, 1994).

The southern rock lobster fishery employs traps with either a single escape gap (57 mm × 400 mm) or two escape gaps (each 57 mm × 200 mm). Compliance with the mandate to equip traps with an escape gap(s) is considered to be excellent, primarily because measuring the gap dimensions is not difficult and commonly performed by enforcement personnel. Compliance with the size regulations is also considered excellent since the penalties for violation are severe, ranging from an A\$200 fine for possession of a single undersized lobster to license forfeiture for possession of 200 or more undersized lobsters. Measurement error is believed to be minimal because fishers use standardized measures certified by the weights and measures authorities to determine the length of captured lobsters.

Tagging protocol

The tagging protocol described by Frusher and Hoenig (2001a) is generally suited for the study contemplated here. However, we offer a few more suggestions that would help minimize the possibility of assumption violation when applying the two-size class model. First, since the new model requires mixing among all tagged cohorts and because rock lobsters have limited movements, it is important to tag at the same fixed locations during each tagging event. Second, it is important that undersized and legal-sized lobsters be treated identically. Ideally, the same person should tag all lobsters captured for a given study; doing so would more easily allow for (if necessary) adjusting for short-term tag-loss and tag-induced mortality. However, since multiple taggers are usually needed to carry out a tagging study, efforts should be directed toward minimizing the heterogeneity among the tagged cohorts (attributed by multiple taggers) to perhaps having the same person tag all captured lobsters on a particular day. In addition, when multiple taggers are employed, the name of each tagger should be recorded so that differences in taggers can be evaluated and, if necessary, adjustments to the data during the analysis can be made. Holding studies would be valuable to evaluate short-term tag-loss and tag-induced mortality, particularly when a tagging program is just beginning.

Need for model simulations

Although the aforementioned tagging study conducted by the Tasmania Aquaculture and Fisheries Institute was designed to obtain estimates of growth rates for the stock assessment model, Frusher and Hoenig (2001a) showed that

the data from the north-western region of the fishery could be analyzed to yield information on mortality. Upon reviewing the available tag-recovery data, we found that insufficient numbers of sublegal-sized lobsters were tagged to utilize the two-size category model that we have developed. We therefore conducted a series of model simulations that were based on the results of previous tag-recovery data analysis efforts to determine the precision that might be obtained with the new model (note that the precision of the natural mortality estimates obtained by Frusher and Hoenig (2001a) was poor).

Simulation design

Frusher and Hoenig (2001a) conducted a comprehensive analysis of rock lobster tag-recovery data from northwest Tasmania, Australia. They combined elements of the instantaneous rates tag-recovery models (Hoenig *et al.*, 1998) with the twice-a-year tagging models (Hearn *et al.*, 1998) to derive estimates of fishing and natural mortality rates and tag-reporting rate. The data analyzed represented tagging efforts from 1992 to 1995 and tag-recovery tabulation from 1992 to 1997. The number of rock lobsters tagged during these years (both sexes combined) ranged from 553 to 1869 and results of the analysis indicated that from 1991 to 1997 fishing mortality rates were high ($F \cong 1.00 - 1.20 \text{ yr}^{-1}$), the natural mortality rate was low ($M \cong 0.00 - 0.10 \text{ yr}^{-1}$), and that tag-reporting was low ($\lambda \cong 0.20 - 0.23$).

To determine if the two-size category model yields biased parameter estimates for sample sizes likely to be used in practice, and also to answer sample size questions as they pertain to precision, we conducted a series of simulations based on the aforementioned values of fishing and natural mortality. Each scenario considered was simulated 5000 times. Scenarios reflecting 5 yr of tagging and tag-recovery with annual cohort sizes of 250, 500, and 1000 lobsters were considered. Natural mortality was held constant over all simulations at 0.05 yr^{-1}; the product $\phi\lambda$ was held constant at 0.21. For each cohort size, fishing mortality rates of 0.5, 1.0, and 1.5 yr^{-1} were chosen and held constant over time. Since the tag-recovery rates are a function of the fishing mortality rates (i.e. Equations (8) and (9) for a Type II fishery), the respective fishing mortality values led to tag-recovery rates of 0.08, 0.13, and 0.16 when the exploitation rates were multiplied by a value of $\phi\lambda$ of 0.21. Program SURVIV (White, 1983) was used to perform all simulations. For all scenarios, a 10-parameter model that specified time-specific tag-recovery and fishing mortality rates and a constant natural mortality rate (i.e. f_1, f_2, f_3, f_4, f_5, F_1, F_2, F_3, F_4, and M) was fit to the data, and for the simulation that specified a tagged cohort size of 1000 lobsters, a fishing mortality rate of 1.0 yr^{-1}, and a tag-recovery rate of 0.13, an additional three-parameter model that reflected constant tag-recovery and fishing mortality rates (i.e. f, F, and M) was fit to the data.

Two additional scenarios were examined to determine if the model could successfully detect changes in the rates of fishing mortality. Assuming an annual tagged cohort size of 1000 lobsters and the aforementioned constant natural mortality rate of 0.05 yr^{-1}, the first scenario specified respective fishing mortality and tag-recovery rates of 1.0 yr^{-1} and 0.13 for years 1–3 and 1.5 yr^{-1} and 0.16 for years 4–5, while the second scenario specified respective fishing mortality and tag-recovery rates of 1.0 yr^{-1} and 0.13 for years 1–2 and 1.5 yr^{-1} and 0.16 for years 3–5. Again, each scenario was simulated 5000 times and only the 10-parameter model was fit to the data.

Results

Simulation results

For each simulation, we examined the mean and standard deviation of the 5000 parameter estimates to assess model performance. We also examined the mean of the 5000 estimated standard errors of each parameter and found that these means were either the same or only slightly larger than the observed standard deviations of the simulation estimates. As such, we discuss precision in the context of the observed standard deviations.

For all simulations, the bias (i.e. the difference between the mean estimate and the true parameter value in magnitude) was negligible, always being less than or equal to 0.02 for both the fishing and natural mortality estimates, and equal to zero for the tag-recovery rate estimates (Tables 1–3). However, the standard deviations of the simulated fishing and natural mortality estimates were not always negligible and, in fact, were quite high when the annual tagged cohort size was only 250 lobsters (Table 1). These standard deviations decreased to more reasonable levels when the annual tagged cohort size increased to 1000 lobsters, which suggests that sample sizes smaller than 1000 tagged lobsters of each size class per year may not be sufficient to obtain precise parameter estimates from the model (Tables 1–3 and Figure 1). Across simulations where the annual tagged cohort size was the same, the standard deviations of the respective fishing and natural mortality estimates increased as the fishing mortality rate increased from 0.5 to 1.5 yr^{-1}. Despite this trend, the loss in precision when the fishing mortality rates were 1.0 and 1.5 yr^{-1} was not substantial enough to prevent qualitative conclusions being made that fishing mortality is high and natural mortality is low.

For the simulations where the true fishing mortality rates changed in years 4–5 and years 3–5, respectively, the standard deviations of the parameter estimates were reasonable and similar to all the simulations that specified a tagged cohort size of 1000 lobsters per year (Table 2). For the scenario in which fishing mortality increased for years 4–5, approximately 50% of the estimated fishing mortality rates in year 4 were between 1.4 and 1.6 (Figure 2). The same is true for the fishing mortality estimates in years 3

Table 1. Simulation results (mean parameter estimates and observed standard deviations) from the time-specific model when the number of tagged lobsters ranged from 250 to 1000 yr^{-1} and three pairs of fishing mortality and tag-recovery rates (0.5 yr^{-1}, 0.08), (1.0 yr^{-1}, 0.13), and (1.5 yr^{-1}, 0.16) were held constant over time. The natural mortality rate was held constant at 0.05 yr^{-1}. The mean tag-recovery rate estimates (not presented here) exactly matched the specified values with a standard deviation less than or equal to 0.06 for all scenarios.

Number tagged	True F	Mean estimate (SD)				
		F_1	F_2	F_3	F_4	M
250	0.5	0.50 (0.23)	0.48 (0.19)	0.49 (0.20)	0.48 (0.24)	0.07 (0.08)
	1.0	1.01 (0.26)	0.98 (0.20)	1.00 (0.20)	0.99 (0.23)	0.07 (0.07)
	1.5	1.52 (0.34)	1.50 (0.24)	1.50 (0.23)	1.50 (0.26)	0.07 (0.07)
500	0.5	0.50 (0.16)	0.49 (0.14)	0.49 (0.15)	0.49 (0.17)	0.06 (0.06)
	1.0	1.01 (0.18)	0.99 (0.14)	0.99 (0.15)	1.00 (0.16)	0.06 (0.06)
	1.5	1.52 (0.23)	1.50 (0.17)	1.50 (0.17)	1.50 (0.18)	0.06 (0.05)
1000	0.5	0.50 (0.11)	0.49 (0.10)	0.49 (0.10)	0.49 (0.12)	0.06 (0.05)
	1.0	1.00 (0.13)	1.00 (0.10)	1.00 (0.10)	1.00 (0.12)	0.05 (0.04)
	1.5	1.50 (0.16)	1.50 (0.12)	1.50 (0.12)	1.50 (0.13)	0.05 (0.04)

and 4 from the scenario in which the fishing mortality rate increased in the final 3 yr of the study (Figure 3). These results, combined with reasonable standard deviations, suggest that the model is able to detect changes in fishing mortality from one year to the next. In the context of lobster management, this is an important characteristic, since the detection of changes in fishing mortality is critical if this model is to be used for the evaluation of management strategies in relation to fishery dynamics.

The standard deviation of the estimate of fishing mortality from the simulation where the fitted model reflected constant tag-recovery, fishing, and natural mortality rates was substantially smaller than those from simulations where the fitted model was time-specific (Table 3). This result suggests that the restricted model can yield reliable parameter estimates, provided it is safe to assume that fishing mortality has not fluctuated substantially over time. However, there was no significant improvement in the precision of the natural mortality estimate from the constant parameter model when compared to that of the time-specific model. In the simulations when the tagged cohort size was 1000 lobsters per year, the standard deviation of the estimated natural mortality rate was 0.04–0.05, regardless of the model parameterization considered.

Discussion

We have developed a two-size category multi-year tag-recovery model that permits direct estimation of instantaneous year-specific fishing and natural mortality rates. A key and extremely attractive characteristic of this model is that these rates of mortality can be estimated in the absence of information on the tag-reporting rate. However, in exchange for this lack of dependence on the tag-reporting rate, it is necessary to make some additional assumptions about the selectivity of the fishery and the size-specific rates of growth and natural mortality of the species under study. At first glance, these assumptions may appear restrictive and unreasonable, and for some fisheries (e.g. those where selectivity varies with size or that involve long-lived species where there may be differential natural mortality rates by age), we acknowledge that this model may not be appropriate. However, for the rock lobster fishery in Tasmania, Australia (and other fisheries with similar characteristics), we contend that these additional assumptions serve only to provide an alternative burden to the researcher, since the uncertainty associated with most tag-reporting rate estimates equally plagues (directly or indirectly) analyses involving the models developed by Seber (1970), Brownie *et al.* (1985), and Hoenig *et al.* (1998).

Table 2. Simulation results (mean parameter estimates and standard deviations) from the time-specific model when the fishing mortality increased from 1.0 to 1.5 yr^{-1} in years 4–5 and years 3–5, respectively. The tag-recovery rates were held constant at 0.13 and 0.16 when the fishing mortality rates were 1.0 and 1.5 yr^{-1}, respectively. The natural mortality rate was 0.05 yr^{-1} and the number of tagged lobsters was fixed at 1000 yr^{-1}. The mean tag-recovery rate estimates (not presented here) exactly matched the specified values with a standard deviation less than or equal to 0.01 for all scenarios.

Number tagged	True F	Mean estimate (SD)				
		F_1	F_2	F_3	F_4	M
1000	$F_4, F_5 = 1.50$	1.00 (0.13)	1.00 (0.10)	1.00 (0.10)	1.50 (0.12)	0.05 (0.04)
1000	F_3–$F_5 = 1.50$	1.00 (0.13)	1.00 (0.10)	1.50 (0.11)	1.50 (0.13)	0.07 (0.05)

Table 3. Simulation results (mean parameter estimates and standard deviations) from the constant parameter model when the tag-recovery and natural mortality rates were held constant at 0.13 and 0.05 yr^{-1}, respectively, and the fishing mortality rate was 1.00 yr^{-1}. The number of tagged lobsters was 1000 yr^{-1}. The mean tag-recovery rate estimate (not presented here) was 0.13 with a standard deviation of 0.004.

	True	Mean estimates (SD)	
Number tagged	F	F	M
1000	1.00	1.00 (0.07)	0.05 (0.04)

If this alternative burden can be absorbed, or at a minimum, if the degree to which violation of these additional assumptions can be characterized, application of this model does possess some unique advantages over other multi-year tag-recovery models. In terms of parameter estimability as a function of the number of tagging and tag-recovery events, the two-size category model systematically yields the most information when compared to that yielded by other tag-recovery models (Table 4). For example, the two-size category model only requires data from one tagging and two tag-recovery events to yield a fishing mortality rate estimate. With all other models, either more years of tagging or additional information about the fishery and/or auxiliary parameters are necessary to obtain such an estimate. Similarly, after 2 yr of tagging and tag-recovery, it is possible to estimate a fishing and natural mortality rate directly from the data with the two-sized category model. Given this amount of data, only the class

of models developed by Hoenig *et al.* (1998) is able to yield similar parameter estimates, provided the tag-reporting rate and the short-term tag-induced shedding/mortality rate are known (note that the Hoenig *et al.* (1998) formulation can yield two fishing and one natural mortality rate if these auxiliary parameters are known).

The simulation results suggest that the model yields accurate parameter estimates. However, the standard deviations of the simulated fishing and natural mortality estimates were unacceptable when the number of tagged lobsters per year was less than 1000. These results suggest that either the annual tagged sample or the tag-reporting rate needs to be increased if the two-size category model is going to be used to derive precise estimates of mortality for the Tasmanian lobster fishery. Of the two, the more likely option is to focus on increasing the tag-reporting rate, since tagging 1000 lobsters per year is currently the limit of what can be accomplished in one cruise in Tasmania.

As expected, when the restricted parameterization of the model was applied, the standard deviation of the estimated fishing mortality rate decreased substantially. Situations where management regulations that specify the same target annual fishing mortality rate have been in place for several years combined with evidence that suggests fishing pressure has not changed substantially over that time period might permit applying this parameterization. Efforts should be made to improve the precision of parameter estimates when applying the two-size category model (and other tag-recovery models), since in some instances a restricted model parameterization may fit the data equally as well as the most general parameterization. As a strategy for data analysis, we suggest fitting a suite of biologically
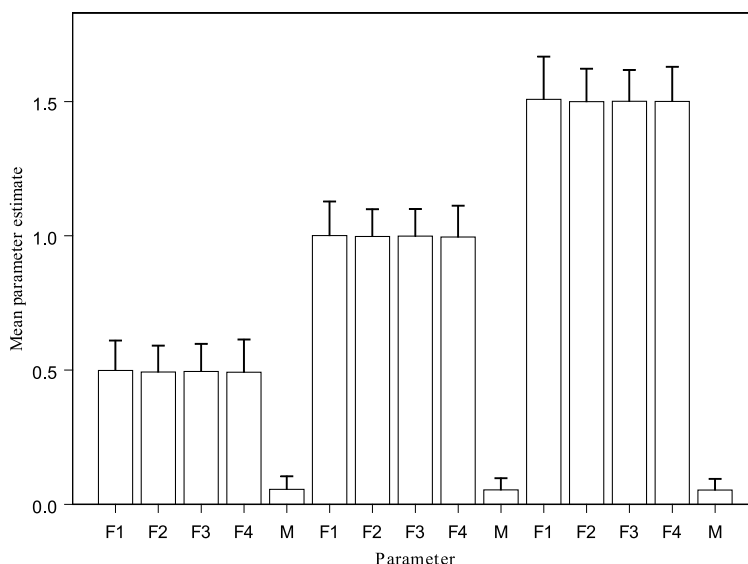
Figure 1. Mean parameter estimates with standard deviations when the time-specific (F_1, F_2, F_3, F_4, M, f_1, f_2, f_3, f_4, and f_5) model was fit to data reflecting 1000 tagged lobsters per year and various levels of fishing mortality. For all simulations, the natural mortality rate was 0.05 yr^{-1} and the tag-recovery rates were 0.08, 0.13, and 0.16 when the fishing mortality rates were 0.5, 1.0, and 1.5 yr^{-1}, respectively.
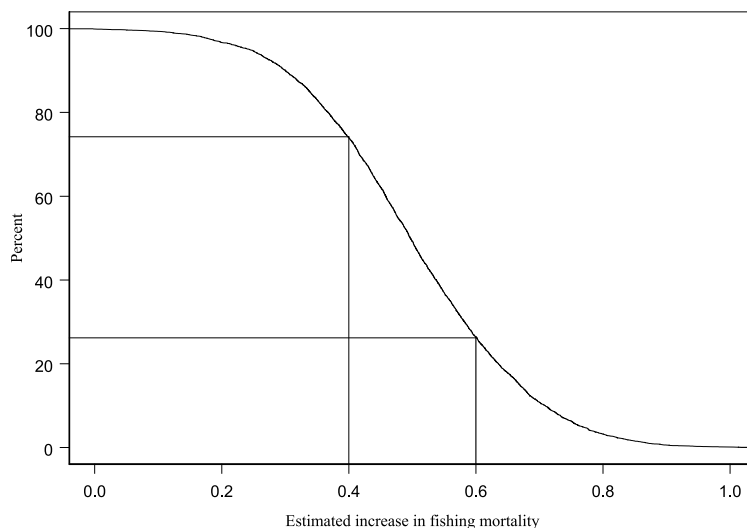
Figure 2. The probability of estimating an increase of a given amount in the year 4 fishing mortality rate when the actual increase was 0.5. The vertical and horizontal lines delineate that there is a 50% chance (75–25%) of estimating an increase of 0.4–0.6 in the fishing mortality rate when the actual increase was 0.5.

reasonable model parameterizations to the data and assessing model fit using model selection techniques based on Akaike's Information Criterion (AIC; Akaike, 1973; Burnham and Anderson, 1992; Burnham *et al.*, 1995) and other related measures such as quasi-likelihood AIC (Akaike, 1985). An inherent benefit of using these model selection techniques is that parameter estimates can be calculated as a weighted average from the results of multiple models rather than from a single "best" model (Buckland *et al.*, 1997; Burnham and Anderson, 1998).

Application to rock lobsters

Here we provide a more detailed discussion of the assumptions of the two-size category model to further evaluate its usefulness as a stock assessment tool for rock lobsters. Our discussion focuses on the new assumptions that are specific to this model, since the potential violation of the standard tag-recovery model assumptions has been characterized previously (Frusher and Hoenig, 2001a).

The structure of the two-size category model specifies that all tagged recruited animals experience the same
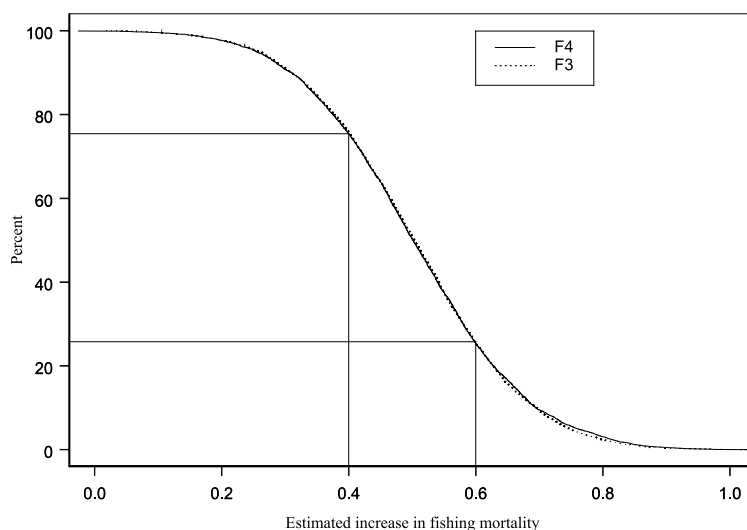

Figure 3. The probability of estimating an increase of a given amount in the fishing mortality rate in years 3 and 4 when the actual increase was 0.5. The solid curve reflects the simulation results for F_3, while the dotted curve depicts that for F_4. As in Figure 2, the vertical and horizontal lines delineate that there is a 50% chance (75–25%) of estimating an increase of 0.4–0.6 in the fishing mortality rate when the actual increase was 0.5.

Table 4. Estimable parameters as a function of the number of years of tagging and tag-recovery from the time-specific parameterizations of several classes of tag-recovery models (refer to text for parameter definitions). Timing refers to knowledge of when during the year the fishery occurs. A Type I fishery (Ricker, 1975) is one in which the fishery occurs as a short pulse at the start of the year. A Type I+ (defined here) is one in which the fishing occurs over a portion of the year (but not the full year) starting at the beginning of the year.

Number of tagging (t) and tag-recovery (r) events	Estimable parameters from model				
	Seber (1970)	Brownie *et al.* (1985)	Hoenig *et al.* (1998)	Hearn *et al.* (1998)	New model
t = 1, r = 1	None	f_1	F_1 given $\phi\lambda$ and Type I	None	f_1
t = 1, r = 2	None	f_1	F_1 given $\phi\lambda$ and Type I	F_1, $\phi\lambda$[a] if Type I; nothing if Type I+	f_1, F_1 given (and $\phi\lambda$ if Type I)
t = 2, r = 2	S_1	S_1, f_1	F_1, F_2, M given $\phi\lambda$ and timing	F_1, M, $\phi\lambda$ for Type I or Type I+	f_1, f_2, F_1, M (and $\phi\lambda$ F_2 given timing)

[a]We include the product $\phi\lambda$ even though the Hearn *et al.* (1998) formulation does not explicitly include the parameter ϕ.

within-year rate of fishing mortality. Frusher and Hoenig (2001b) examined southern rock lobster selectivity in Tasmania and demonstrated that the selectivity of lobsters changes with size and during the fishing season in response to the removal of larger lobsters. With respect to the potential application of the two-size category model presented herein, these findings imply that the same narrow range of sizes of lobsters should be tagged each year. For pre-recruited lobsters, the idea of a narrow size range is already inherent to the model formulation, since all pre-recruited lobsters that are tagged are assumed to be within one growth increment of the legal size limit (Figure 4).

The model also specifies that all animals (pre-recruited or recruited) experience the same within-year rate of natural mortality. This assumption is not likely to be violated since studies have shown that the natural mortality rate for rock lobsters near or above the legal size limit is very low ($\cong 0.05$ yr^{-1}, see Frusher and Hoenig, 2001a) and is unlikely to vary substantially with size since the size classes defined near the legal size limit are likely to be narrow.

The last of the newly introduced assumptions requires knowledge of rock lobster growth, since a lower size limit for the pre-recruits must be defined knowing that lobsters within that size class will be of legal size after 1 yr at liberty. Growth of rock lobsters in Tasmania varies substantially over space and between sexes. Molting is relatively synchronized with similar sized lobsters molting at approximately the same time in the same region. Male lobsters at or near the legal size limit molt from August to
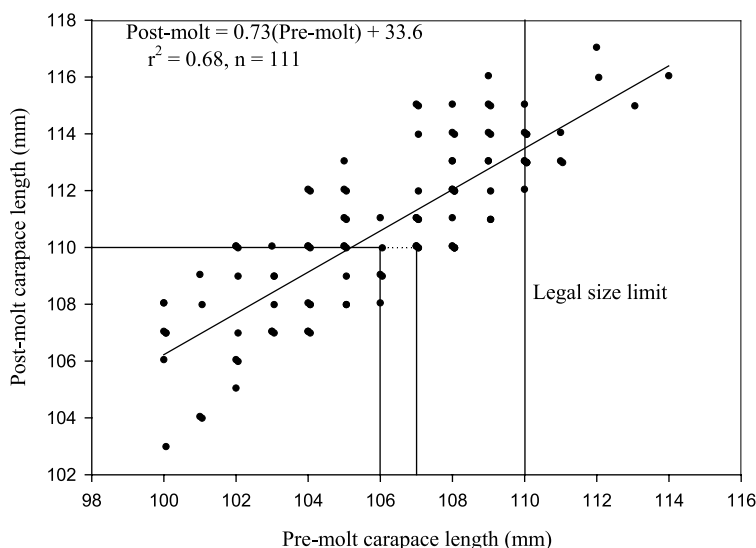

Figure 4. Incremental growth data derived from capture/recapture studies conducted on male rock lobsters that were at liberty 350–365 days in southern Tasmania from 1992 to 2000. A simple linear regression model was fit to the data to describe post-molt size as a function of pre-molt size. Note that if the lower size limit for the pre-recruited size class is set at 107 mm CL, the assumption that these animals will grow to become legal-sized (110 mm CL) in 1 yr will be met. The data were jittered slightly for display.

November in southern Tasmanian and somewhat later in northern Tasmania (Frusher, 1997). Female rock lobsters in the same respective areas molt from April to May and generally have slower growth rates than males. The fishing season commences in November (normally mid-November but the actual date has changed over time) when both sexes are fished. The female fishing season closes at the end of April in anticipation of their molting season. Females caught in traps from May to August when it is still legal to capture males are released to the sea. The male fishing season is open from November to August of the following year. Males then molt during the closed period of September/October and the subsequent fishing season has access to full recruitment to the fishery.

To determine a suitable lower size limit for the pre-recruited size class, we examined growth increment data from capture/recapture studies conducted on male rock lobsters in southern Tasmania from 1992 to 2000. Growth data from lobsters that were tagged in November and recaptured the following November just before the fishing season (time at liberty ranged from 350 to 365 days) were considered. A simple linear regression model was developed to describe post-molt size as a function of pre-molt size, and also to assess the probability of growing to the legal size limit of 110 mm CL within one molt (Figure 4). The results of the analysis suggest that if the lower size limit for the pre-recruited size class is set at 107 mm CL, the assumption that these animals will grow to become legal sized (110 mm CL) in 1 yr will be met. However, a lower limit of 107 mm CL presents a narrow size range for the pre-recruited group, which, in turn, raises sample size issues since it may not be possible to tag an adequate number of lobsters between 107 and 109 mm CL. A lower limit of 106 mm CL would reduce sample size problems, but the growth data indicate that not all pre-molt lobsters that are 106 mm CL grow to legal size in 1 yr (only two out of five reached or exceeded the 110 mm CL legal size limit).

To accommodate the problems that arise from variable growth rates, we generalized the model presented in Equation (2) to allow the transition to the fully recruited size class to take more than 1 yr (Appendix). To apply this model formulation, it is necessary to know the number of years required for the pre-recruited size class to grow to legal size, and the probability of growing to that size after each of those years, given that the growth probability in the final year is 1.0. Although the generalization in Appendix A is formulated under the assumption that the transition to the fully recruited size class requires only 2 yr, it should be noted that the model can be adjusted to accommodate a longer transition.

Acknowledgements

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Appendix

Model generalization allowing for variable growth

For some populations, growth may be highly variable and it may not be possible to identify an obvious minimum size above which all tagged animals will grow to the legal limit after 1 yr at liberty. To accommodate this situation, we have developed a generalization to the two-size category model that allows for variable growth rates among the individuals in the pre-recruited size class. For ease of display, the case where the transition to the fully recruited size class takes at most 2 yr is presented. However, the expected cell probabilities of the model can be easily modified to allow this transition to take more than 2 yr if necessary.

To develop the generalization, let the parameter g represent the fraction of the pre-recruited animals that reaches legal size after 1 yr at liberty (note that g must be estimated externally). The remaining pre-recruits are assumed to reach legal size after one more year. The matrix of tag-recoveries for a study with I yr of tagging and J yr of tag-recovery for the generalized model is exactly the same as that of the original model (refer to Equation (1)). However, the matrix of expected values is not identical, since the expected number of tag-recoveries associated with the pre-recruited cohorts must be adjusted to account for the transition to the recruited size class taking up to 2 yr. The matrix of expected values corresponding to Equation (1) under a time-specific parameterization is:

$$
E(R) = \begin{bmatrix}
N_{1r}f_1 & N_{1r}\,e^{-(F_1+M_1)}f_2 & N_{1r}\,e^{-(F_1+F_2+M_1+M_2)}f_3 & \cdots & N_{1r}\,e^{-\sum_{k=1}^{J-1}(F_k+M_k)}f_J \\[2mm]
0 & gN_{1p}\,e^{-M_1}f_2 & N_{1p}\left(\begin{array}{l}g\,e^{-(F_2+M_1+M_2)}+\\(1-g)\,e^{-(M_1+M_2)}\end{array}\right)f_3 & \cdots & N_{1p}\left(\begin{array}{l}g\,e^{-\sum_{k=2}^{J-1}F_k-\sum_{k=1}^{J-1}M_k}+\\(1-g)\,e^{-\sum_{k=3}^{J-1}F_k-\sum_{k=1}^{J-1}M_k}\end{array}\right)f_J \\[2mm]
- & N_{2r}f_2 & N_{2r}\,e^{-(F_2+M_2)}f_3 & \cdots & N_{2r}\,e^{-\sum_{k=2}^{J-1}(F_k+M_k)}f_J \\[2mm]
- & 0 & gN_{2p}\,e^{-M_2}f_3 & \cdots & N_{2p}\left(\begin{array}{l}g\,e^{-\sum_{k=3}^{J-1}F_k-\sum_{k=2}^{J-1}M_k}+\\(1-g)\,e^{-\sum_{k=4}^{J-1}F_k-\sum_{k=2}^{J-1}M_k}\end{array}\right)f_J \\[2mm]
\vdots & \vdots & \vdots & \ddots & \vdots \\[1mm]
- & - & - & \cdots & y_r \\[1mm]
- & - & - & \cdots & y_p
\end{bmatrix}
\tag{A1}
$$

The expected value corresponding to the (I,J,r) cell is the same as that defined by Equation (3), while the expected value corresponding to the (I,J,p) cell is

$$
y_p = \begin{cases}
0 & \text{if } I = J, \\[2mm]
gN_{Ip}\,e^{-M_I}f_J & \text{if } J = I+1, \\[2mm]
N_{Ip}\left(g\,e^{-\sum_{k=I+1}^{J-1}F_k-\sum_{k=I}^{J-1}M_k}+(1-g)\,e^{-\sum_{k=I+2}^{J-1}F_k-\sum_{k=I}^{J-1}M_k}\right)f_J & \text{otherwise.}
\end{cases}
\tag{A2}
$$

For populations that have not been well studied, it may be difficult to obtain information on growth and ultimately an estimate of g. However, for populations that are formally managed, information on growth and other types of fundamental biological data is generally available. As such, the additional requirement to derive an external estimate of g should not be problematic.