



Recent developments in estimating fishing and natural mortality and tag reporting rate of lobsters using multi-year tagging models

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Abstract

From May 1992 to May 1995, tagging of southern rock lobster, *Jasus edwardsii*, was undertaken in May, February and September in northwestern Tasmania, Australia. Previous modelling of these data using multi-year tagging models produced estimates of annual fishing mortality and tag reporting rates with low relative standard errors and a very low natural mortality estimate (0.0) with high relative standard error. In this model, natural mortality was partitioned within a year by the duration of the time periods and fishing mortality was partitioned by the proportion of fishing effort expended during each period. We altered the model to take advantage of quantitative information on the amount of fishing effort. In the new models, fishing mortality (F) was replaced by catchability (q) multiplied by fishing effort (e) (i.e., $F = qe$). The most parsimonious model was based on constant catchability over years with unequal catchability among periods within a year. A model with separate catchabilities for each sex did not improve the model. Annual fishing mortality and tag reporting rate estimates had low relative standard errors and were similar to the previous model. The natural mortality estimate (0.12 per year) was higher and more precise than in the previous model and similar to previously published values. Based on Akaike's information criterion (AIC), we found the model based on effort (i.e., $F = qe$) to be superior to previous models that used effort information merely to apportion fishing mortality to periods of the year. Comparison of the residuals between the two models demonstrated that the inclusion of effort in the model reduced problems with patterns in the residuals.

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1. Introduction

Brownie et al. (1985) presented a series of multi-year tagging models aimed at estimating survival of animals tagged over successive years. Essentially, the expected number of recoveries is the product of the number tagged, the fraction that has survived up to the harvest period and the fraction of tags recovered and reported during the harvest period (Table 1).

Hoenig et al. (1998) re-parameterised the multi-year tagging models of Brownie et al. (1985) in a very general formulation that expresses survival in terms of instantaneous rates of fishing and natural mortality. The survival term in year i (S_i) was replaced by $S_i = \exp(-F_i - M_i)$. The recovery rate term (f_i) depends on the timing (seasonal pattern) of the fishing effort. When fishing intensity is constant over the year, f_i is replaced by

$$\lambda(1 - \exp(-F_i - M_i)) \left(\frac{F_1}{F_1 + M_1} \right) \quad (1)$$

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Table 1
Expected recoveries of tagged animals during 4 years of harvesting from animals tagged at the start of the first 3 years (from Brownie et al., 1985)^a

Year	Expected recoveries			
	Year 1	Year 2	Year 3	Year 4
1	$N_1 f_1$	$N_1 S_1 f_2$	$N_1 S_1 S_2 f_3$	$N_1 S_1 S_2 S_3 f_4$
2		$N_2 f_2$	$N_2 S_2 f_3$	$N_2 S_2 S_3 f_4$
3			$N_3 f_3$	$N_3 S_3 f_4$

^a f_i : probability that a tagged animal, alive at the start of year i , is recaptured and reported during year i ; S_i : probability an animal, alive at the start of year i , survives the year; N_i : number of animals tagged at the start of year i .

where F_i is the instantaneous fishing mortality rate in year i , M_i the instantaneous natural mortality rate in year i , λ a composite parameter that represents the joint probability of three events: the probability that a tag will be found and reported to the fisheries biologist, given that the tagged animal has been harvested; the probability that a tagged animal does not die from the tagging process; and the probability that a tag is not shed immediately. λ is assumed constant over time.

The term $(1 - \exp(-F_i - M_i))$ in Eq. (1) represents the fraction of animals alive at the start of period i that dies in the period. The term $F_1/(F_1 + M_1)$ in Eq. (1) is the fraction of the deaths attributable to fishing in year i .

Substituting for S and f in Table 1, we obtain the following expected recoveries over time for the animals tagged at the start of the first year:

$$N_1 f_1 = N_1 \lambda (1 - \exp(-F_1 - M_1)) \left(\frac{F_1}{F_1 + M_1} \right),$$

$$N_1 S_1 f_2 = N_1 \exp(-F_1 - M_1) \lambda (1 - \exp(-F_2 - M_2)) \times \left(\frac{F_2}{F_2 + M_2} \right),$$

$$N_1 S_1 S_2 f_3 = N_1 \exp(-F_1 - M_1 - F_2 - M_2) \lambda \times (1 - \exp(-F_3 - M_3)) \left(\frac{F_3}{F_3 + M_3} \right)$$

These expectations can be converted into a set of probabilities for a tag being recovered in any particular year. The tag recoveries from a cohort of tagged animals thus represent a sample from a multinomial distribution.

In practice, the natural mortality rate is assumed not to vary over time and $M_i = M$ for all years i in order to reduce the number of parameters in the model. Although tag reporting rate (λ) can theoretically be estimated from the models, Hoenig et al. (1998) found that tag reporting rate estimates were unreliable (even if M is assumed constant over all years) unless there are many years of tagging with a wide range of fishing mortality rates.

Hearn et al. (1998) described a model that used data from a twice-a-year tagging study to estimate fishing and natural mortality. They were also able to obtain improved estimates of tag reporting rate over that obtainable from the models of Hoenig et al. (1998). The Hearn et al. (1998) model has a fishing period where both fishing and natural mortality affect survival and a closed period of the year where only natural mortality affects survival. For example, if we assume that a fishing season operates for 6 months of the year and we tag at the start of the fishing season (s) and also at the end of the fishing season (e) we obtain the expected recoveries in Table 2.

To demonstrate how the parameters can be estimated, we use the example in Table 2. If we divide the expected returns in year 2 from tagging at the end of the fishing season in year 1 by the expected returns in year 2 from tagging at the start of the fishing season in year 2 we get

$$\frac{N_{1e} \lambda \exp(-0.5M_1) (1 - \exp(-F_2 - 0.5M_2)) \times (F_2/(F_2 + 0.5M_2))}{N_{2s} \lambda (1 - \exp(-F_2 - 0.5M_2)) (F_2/(F_2 + 0.5M_2))} = \frac{N_{1e} \exp(-0.5M_1)}{N_{2s}}$$

If this is equated with the ratio of tag recoveries from these two cohorts the result is easily solved for an estimate of M_1 .

By dividing the expected recaptures in year 2 from tagging at the start of year 1 by the expected recaptures (in year 2) from tagging at the end of year 1 we get

$$\frac{N_{1s} \lambda \exp(-F_1 - M_1) (1 - \exp(-F_2 - 0.5M_2)) \times (F_2/(F_2 + 0.5M_2))}{N_{1e} \lambda \exp(-0.5M_1) (1 - \exp(-F_2 - 0.5M_2)) \times (F_2/(F_2 + 0.5M_2))} = \frac{N_{1s} \exp(-F_1 - M_1)}{N_{1e} \exp(-0.5M_1)}$$

Table 2
Expected recoveries from tagging twice per year at the start (s) and end (e) of the harvesting period^a

Year	Tagging period	Expected recoveries	
		Year 1	Year 2
1	s	$N_{1s}\lambda(1 - \exp(-F_1 - 0.5M_1)) \left(\frac{F_1}{F_1 + 0.5M_1} \right)$	
	e	$N_{1e}\lambda \exp(-0.5M_1)(1 - \exp(-F_2 - 0.5M_2)) \left(\frac{F_2}{F_2 + 0.5M_2} \right)$	
2	s	$N_{2s}\lambda(1 - \exp(-F_2 - 0.5M_2)) \left(\frac{F_2}{F_2 + 0.5M_2} \right)$	

^a This example assumes that the harvesting period is for 6 months of the year and that natural mortality in a time interval is proportional to the length of the interval. Thus for 6 months of the year, both fishing mortality and natural mortality affect survival and for 6 months of the year only natural mortality affects survival. N_{ik} is the number of lobsters tagged in year i and tagging period k or $k = \{s, e\}$. F_i and M_i are the instantaneous fishing and natural mortality rates, respectively, in year i . λ is a composite parameter that includes tag reporting rate, tag loss and tag-induced mortality.

Again, if this is equated with the observed ratio of recaptures from the two cohorts the result is easily solved for an estimate of F_1 when M_1 is known.

Substituting estimated values for F_1 and M_1 into the expected recaptures in year 1 from tagging at the start of year 1 and equating with the observed number of recaptures allows estimation of λ .

Frusher and Hoenig (2001a) combined the approaches of Hoenig et al. (1998) and Hearn et al. (1998) and applied the method to the data from the fishery for southern rock lobster (*Jasus edwardsii*) in Tasmania, Australia. In their models, information on fishing effort was used merely to apportion the total fishing mortality in a year to periods of the year. Information on fishing effort was not functionally linked to year to year changes in mortality (so that a doubling of fishing effort from 1 year to the next did not force the predicted fishing mortality to be doubled). Hoenig et al. (1998) termed this use of fishing effort data the “weak effort assumption”. They

also suggested that annual fishing mortality might be modelled as being proportional to fishing effort, and termed this the “strong effort” assumption. Latour et al. (2001) applied this idea in the context of the models of Hoenig et al. (1998). However, their data were sparse and their results were highly dependent on externally supplied information of tag reporting rate. Consequently, they were not able to develop and compare a suite of competing models. In this paper we explore a variety of models relating fishing mortality to fishing effort in the general context of the models of Hoenig et al. (1998) and Hearn et al. (1998). The models were developed to deal with the practical issues presented by the rock lobster data set.

2. Model extensions and evaluation

Rock lobsters were tagged in northwestern Tasmania from May 1992 to May 1995. Tagging was

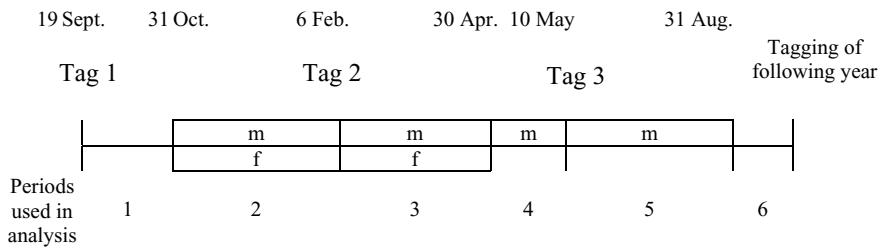


Fig. 1. Division of the 1992/1993 fishing year into six periods according to fishing regulations and presence of tagged cohorts. The symbols m and f represent the periods when the fishery is open for males and females, respectively. Tags 1–3 indicate releases of tagged cohorts.

undertaken three times within a year: in September, just prior to the opening of the fishing season; in February, mid-way through the fishing season; and in May after the end of the female fishing season. This experimental design led to consideration of six periods of the year defined by the cohorts available to be caught and the sexes for which the fishery was open (Fig. 1).

We apportioned fishing mortality within the fishing year to time period by the proportion of fishing effort expended during the period. Natural mortality was apportioned to period based on the length of the time period (see Hoenig et al., 1998; Frusher and Hoenig, 2001a). For example, in the 1992/1993 fishing year (Table 3), tagging was undertaken on 19 September. The lobsters were subject to only natural mortality for the period from 20 September to 31 October (period 1) before being available for harvesting from the 1 November to 6 February (period 2). During period 2, 39.2% of the fishing effort during the male season occurred; 49.4% of the effort during the female season occurred. Although natural mortality may vary within a year (e.g., with moulting), the models are not sensitive to the timing of natural mortality (Hoenig et al., 1998). Allowing natural mortality to vary within a year would overparameterise the tagging models used.

Due to the large number of parameters to be estimated, tag reporting rate, λ , and natural mortality rate, M , were held constant over all years. To further reduce the number of parameters and make use of auxiliary data on fishing effort, we substituted the equation $F_{ijk} = q_{jk}e_{ij}$ for each of the F 's in the basic model. Here, F , q and e represent fishing mortality, catchability and effort, respectively, and the subscripts i , j and k refer to the year, period of the year and sex, respectively.

To minimise the number of parameters being estimated, we kept catchability constant for the same period of the year among different years. Four models for catchability and effort were evaluated (Table 4). The most parameterised model, Model 1, estimated three seasonal catchability parameters for males (November–February, February–May and May–August) and two seasonal catchability parameters for females (November–February and February–April) as the female fishing season is closed from May to August during the male fishing season. The next most parameterised model, Model 2, had three seasonal catchability parameters with catchabil-

ity of males assumed equal to that of females. The third model assumed no seasonal variation in catchability and estimated a single catchability for each sex separately. The least parameterised model, Model 4, assumed no seasonal or sex-specific variation in catchability and estimated a single catchability parameter. Maximum likelihood parameter estimates were obtained for each model using the program SURVIV (White, 1983).

Initial model selection was based on parsimony. Burnham and Anderson (1998) describe parsimony as the concept that a model should be as simple as possible with respect to the model structure and number of parameters while still fitting the data well. This strategy compares the improvement in fit of models with increased numbers of parameters to the most parsimonious model. Only models with a substantial improvement in fit are considered more appropriate than the parsimonious model. Following the procedures of Burnham and Anderson (1998), we used weighted Akaike's information criterion (wQAIC) to formally select models after accounting for over-dispersion of the data. Data is considered to be over-dispersed if the χ^2 value is greater than 2 after being divided by the degrees of freedom for the model. The most parsimonious of the models tested is the model with the highest wQAIC value. To determine the extent to which other models are appropriate, the wQAIC value of the most parsimonious model is divided by the wQAIC value of the model of interest. The resultant value indicates the support for that model (Burnham and Anderson, 1998). For example, in Table 4 the most parsimonious model (season, Model 2) has 1.5 times more support than Model 1 (season \times sex). Burnham and Anderson (1998) state that models with a support value of less than 2 should be considered as plausible models.

Annual fishing mortalities were obtained by summing the products of seasonal catchability and effort:

$$F_{\text{year}} = q_a e_a + q_b e_b + q_c e_c \quad (5)$$

where a is the November–February, b the February–May and c the May–August.

To evaluate the fit of the most parsimonious of the models based on the strong effort assumption to the data we analysed the residuals for patterns that would indicate the problems described by Latour et al. (2001). To identify differences in fit between the most parsimonious of the models based on the strong effort

Table 3

Apportionment of fishing mortality to period of time based on fishing effort (pot lifts) and apportionment of natural mortality to period based on duration (days) (from Frusher and Hoenig, 2001a)^a

Fishing year	Units	Sex	Periods used in analysis					
			1	2	3	4	5	6
1991/1992	Dates						11 May–31 August	1 September–19 September
	Pot lifts	M					0.17	0
		F					0	0
	Day					0.31	0.052	
1992/1993	Dates		20 September–31 October	1 November–6 February	7 February–31 April	1 May–10 May	11 May–31 August	1 September–19 September
	Pot lifts	M	0	0.392	0.402	0.029	0.177	0
		F	0	0.494	0.506	0	0	0
	Day		0.115	0.271	0.225	0.027	0.31	0.052
1993/1994	Dates		20 September–17 November	18 November–13 February	14 February–31 April	1 May–10 May	11 May–31 August	1 September–19 September
	Pot lifts	M	0	0.379	0.366	0.026	0.228	0
		F	0	0.509	0.491	0	0	0
	Day		0.164	0.238	0.208	0.027	0.31	0.052
1994/1995	Dates		20 September–17 November	18 November–29 January	30 January–31 April	1 May–22 May	23 May–31 August	1 September–19 September
	Pot lifts	M	0	0.235	0.422	0.082	0.261	0
		F	0	0.358	0.642	0	0	0
	Day		0.164	0.197	0.249	0.06	0.277	0.052
1995/1996	Dates		20 September–30 November	1 December–6 February	7 February–31 April	1 May–10 May	11 May–31 August	1 September–19 September
	Pot lifts	M	0	0.268	0.415	0.041	0.275	0
		F	0	0.392	0.608	0	0	0
	Day		0.197	0.189	0.227	0.027	0.309	0.052
1996/1997	Dates		20 September–17 November	18 November–6 February	7 February–31 April	1 May–10 May	11 May–31 August	1 September–19 September
	Pot lifts	M	0	0.308	0.318	0.023	0.351	0
		F	0	0.492	0.508	0	0	0
	Day		0.164	0.222	0.225	0.027	0.310	0.052

^a Except for the 1991/1992 fishing year, where data are incomplete, the entries in a row add up to 1.000. Periods used in the analysis are: (1) first tagging to start of fishing season; (2) open season for males and females to second tagging; (3) second tagging to close of female season; (4) close of female season to third tagging; (5) third tagging to close of male season; (6) close of male season to first tagging of the next year.

Table 4

Number of parameters (p), dispersion coefficients (\hat{c}), Δ QAIC values, AIC weights (wQAIC), and level of support for four models based on three tagging events per year^a

Model	p	\hat{c}	Δ QAIC	wQAIC	Support
1 (season \times sex)	7	2.04	0.80	0.40	1.50
2 (season)	5	2.05	0.00	0.60	1.00
3 (sex)	4	2.47	36.64	0.00	9×10^7
4 (no season or sex)	3	2.47	36.37	0.00	7×10^7
Frusher and Hoenig (2001a)	8	2.11	5.36	0.04	14.59

^a Models 1–4 replace instantaneous fishing mortality (F) in the Frusher and Hoenig (2001a) model with the product of catchability and fishing effort (qf). Catchability varies in Model 1 by season and sex, in Model 2 by season, and in Model 3 by sex; catchability did not vary by season or sex in Model 4. A single natural mortality rate (M) and tag reporting rate (λ) are estimated in all models. A Δ QAIC value is an AIC value after accounting for over-dispersion of the data (see Burnham and Anderson, 1998 for further details). Models with support values less than 2 are considered plausible models.

assumption to the most parsimonious model using the weak effort assumption (Frusher and Hoenig, 2001a) we compared the residuals of both models as well as the wQAIC values.

3. Results and discussion

Frusher and Hoenig (2001a) found the most parsimonious model utilising the weak effort assumption

for estimating annual fishing mortalities was based on combined sexes. Their model produced reasonably precise estimates of fishing mortality and tag reporting rate but an imprecise and extremely low estimate of natural mortality (Fig. 2).

Frusher and Hoenig (2001a) were concerned that the relative precision of their estimates of fishing mortality began to decline after tagging stopped (1995/1996 and 1996/1997 fishing years). They considered this to be due to the low number of tags available for recapture because of the high exploitation rates in the fishery.

Although fishing mortality rates are apportioned to the period of the year by relative fishing effort in the models of Frusher and Hoenig (2001a), the models did not force annual fishing mortality to be proportional to annual fishing effort. If there is a strong relationship between effort and fishing mortality, it would be worthwhile to take advantage of this additional information. However, to do so would require specification of a model relating the two variables. The simplest model assumes a sex- and time-invariant proportionality. However, Ziegler et al. (2002) found catchability to change throughout the fishing season with a high value in spring/summer and a low value in autumn/early winter. Thus the timing of fishing effort within a fishing season and between fishing seasons will influence the number of lobsters captured and thus the probability of tagged lobsters being caught.

To determine if variability in catchability is influencing estimation of fishing and natural mortality rates

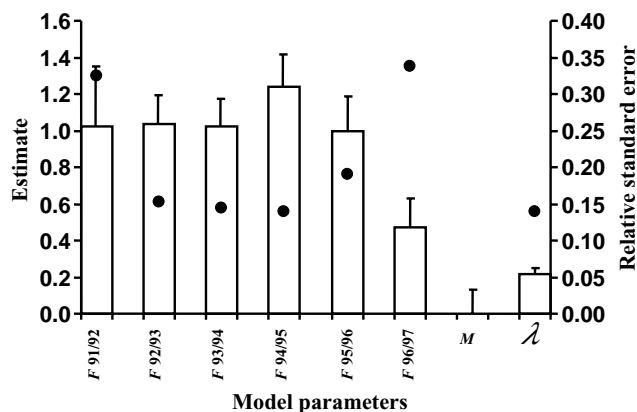


Fig. 2. Estimates of annual fishing mortality (F_i) from 1991/1992 to 1996/1997, natural mortality (M) and tag reporting rate (λ) based on the model of Frusher and Hoenig (2001a). Error bars are 1 standard error. The relative standard errors (closed circles) are presented for each estimate except M where the relative standard error is infinite.

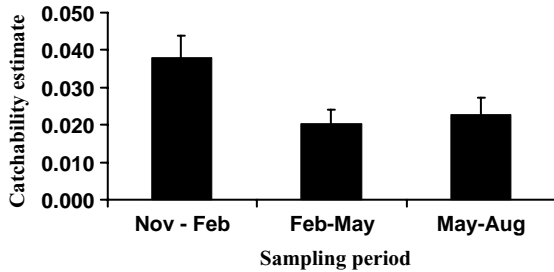


Fig. 3. Seasonal catchability estimates from Model 2 with three tagging periods per fishing year. Catchability of males is set equal to catchability of females. Error bars are 1 standard error.

and tag reporting rate we tested four models with fishing mortality replaced by the product of seasonal effort and catchability. Of the four models tested, the most parsimonious model was when a non-sex-specific q was estimated separately for each period (Model 2, Table 4). Model 1, with seasonal estimates of q for each sex was also supported. However, this model required two extra parameters that did not appear to improve the fit. There was no support for holding q constant within a fishing year either with or without a sex effect (Models 3 and 4, respectively). The most parsimonious model using the strong effort assumption (Model 2) had over 14 times more support than the most parsimonious of the weak effort assumption models of Frusher and Hoenig (2001a).

The conclusion that catchability changes seasonally was consistent with the findings of Ziegler et al. (2002). A similar trend in catchability was obtained in this study with a high in the November–February period followed by a low in February–May and a slight increase from May to August (Fig. 3).

Fishing mortality estimates from the weak (Frusher and Hoenig, 2001a) and strong (Model 2) effort assumptions were similar for the fishing years while tagging was ongoing (1992/1993 to 1995/1996, Fig. 4). Although substantial seasonal changes in catchability were estimated (February–May being nearly half of November–February, Fig. 3), Ziegler et al. (2002) found catchability of lobsters in Tasmania to be related to three primary factors: changes in water temperature (summer to winter), moulting and mating. As these factors occur at relatively similar times from year to year, catchability estimates can be used to estimate fishing mortality beyond the years of tagging.

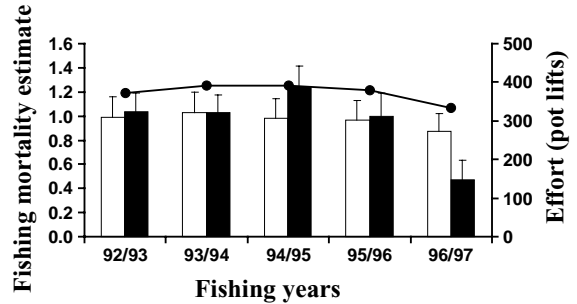


Fig. 4. Comparison of fishing mortality estimates from a tagging model with the weak effort assumption (Frusher and Hoenig, 2001a) (solid bars) and Model 2 with the strong effort assumption and seasonally varying catchabilities (open bars), and to total fishing effort within each year (closed circles). Error bars are standard errors.

The estimated fishing mortality for the terminal year from Model 2 reflects the amount of fishing effort; in contrast, the model of Frusher and Hoenig (2001a), based on the weak effort assumption, does not link the mortality to the effort. If fishing mortality is indeed strongly linked to fishing effort, then Model 2 is appropriate and leads to increased precision.

Natural mortality estimates from Model 2 (0.12, S.E. = 0.14) were similar to the 0.1 per year value used by Punt and Kennedy (1997) for modelling the Tasmanian rock lobster fishery. Although natural mortality is unknown, the estimates from Model 2 are considered an improvement over the zero estimates of Frusher and Hoenig (2001a). Unlike fishing mortality, natural mortality estimates appear to be more sensitive to the way effort is incorporated into the model.

The estimate and precision of tag reporting rate was similar for both the weak (0.22, S.E. = 0.03) and strong effort (0.25, S.E. = 0.04) assumption models. Frusher and Hoenig (2001a) examined the residuals of their most parsimonious model for patterns as described by Latour et al. (2001). Examination of the residuals for the most parsimonious model based on the strong effort assumption found no systematic pattern in the sign of the residuals for rows (this sometimes indicates a bad tagger or a tagging episode with bad tagging conditions) or for the main diagonal or upper right corner that would indicate a problem with non-mixing or emigration (Table 5). As with the residuals of the weak effort assumption model, the strong

Table 5
Recapture residuals (observed–expected recaptures) of male and female legal sized lobsters from May 1992 to September 1997 for Model 2, which allows catchability to vary by season^{a,b}

Year/ timing	Tag date	Sex	Number tagged	Recapture period																	
				1992 ^c			1993			1994			1995			1996			1997		
				September	February ^d	May ^e	September	February	May	September	February	May	September	February	May	September	February	May	September	February	May
1/a	May 1992	M	333	-1.1	2.0	11.1	0.7	-4.0	2.2	-0.8	-2.2	-0.5	1.4	-0.7	-0.5	-0.2	-0.2	-0.1	-0.1		
		F	220		12.5	3.0		0.3	-1.4		-1.7	-0.7		-0.1	-0.7		0.5	-0.2			
2/b	September 1992	M	486		9.0	5.2	-3.0	0.4	6.1	2.6	0.0	-0.7	0.0	-1.3	0.2	1.6	-0.4	-0.2	-0.2		
		F	577		15.5	-2.5		-2.2	4.7		4.6	-1.5		-2.1	0.1		0.6	-0.6			
2/d	February 1993	M	280			-5.8	-1.6	-8.0	3.4	-2.2	5.2	-0.6	0.0	-0.2	-0.8	1.6	-0.4	-0.2	-0.2		
		F	240			-6.9			1.4	0.6	5.9	3.9		-2.1	-1.3		0.1	0.6			
2/a	May 1993	M	181				-4.2	7.8	2.8	-3.0	0.4	0.6	0.1	1.8	-0.8	-0.4	-0.4	-0.2	0.9		
		F	105					7.8	4.0		1.8	-1.0		2.7	0.2		-0.6	1.7			
3/b	September 1993	M	226					-5.6	-3.7	-3.7	0.4	-0.8	7.6	-0.8	-0.2	-0.6	0.4	-0.3	-0.2		
		F	228					0.3	0.9		-3.2	0.5		1.0	0.2		-1.3	-0.6			
3/d	February 1994	M	357						-3.5	-12.4	2.3	-4.0	2.2	-2.8	-1.1	1.5	-1.6	-0.8	-0.6		
		F	323							-7.5	3.9	-4.5		-0.2	-0.4		-2.1	0.5			
3/a	May 1994	M	229							-6.5	2.4	3.8	4.5	-2.4	2.1	1.6	-1.5	0.3	-0.5		
		F	154								-0.4	-2.0		-2.8	-0.9		-1.1	-1.0			
4/b	September 1994	M	168								-1.0	7.1	1.6	-2.2	0.3	0.6	-1.4	-0.7	0.5		
		F	224								-9.3	0.3		-0.3	-2.4		-2.2	-1.5			
4/d	January 1995	M	267									-4.4	-2.1	-2.3	-3.7	6.7	-2.4	-1.7	-1.3		
		F	230									2.3		-4.4	-1.9		7.0	-1.4			
4/a	May 1995	M	159										0.6	1.6	0.9	8.0	-3.1	-1.6	0.8		
		F	94											-3.8	-1.1		-3.0	-1.4			

^a a: after female fishing year, b: before start of male and female fishing year and d: during female and male fishing year. Blank spaces in the recapture part of the table indicate that no fishing occurred for that sex for that period in time.

^b Negative residuals are in bold.

^c The period from mid-May to mid-September.

^d The period from mid-September to mid-February.

^e The period from mid-February to mid-May.

Table 6
Summed values of residuals over: (a) sex, (b) tagging periods and (c) recapture periods for the most parsimonious model based on the strong effort assumption (F replaced by qf) and the weak effort assumption model of Frusher and Hoenig (2001a)^a

Model	All	Male	Female
(a) Sex			
F (weak effort)	-0.42	20.68	-21.1
qf (strong effort)	0.854	-1.591	2.445
(b) Tagging periods			
F (weak effort)			
September	1.3	24.6	-23.3
February	-33.8	-33.8	0
May	32.1	29.9	2.2
qf (strong effort)			
September	15.5	16.7	-1.2
February	-48.4	-41.7	-6.7
May	33.8	23.4	10.4
(c) Recapture periods			
F (weak effort)			
May–September	1.0	1.0	
September–February	101.1	53.3	47.8
February–May	-102.5	-33.6	-68.9
qf (strong effort)			
May–September	0.2	0.152	
September–February	11.6	-11.118	22.7
February–May	-10.9	9.375	-20.3

^a “All” refers to the sum over all rows and columns (but excludes the residuals for the never-seen-again categories).

effort assumption model did have some column effects where most of the residuals in a column were of the same sign. We suspect this might indicate a random fluctuation in catchability or natural mortality over time. There were also some rows with a preponderance of residuals of one sign. If this were due to a bad tagger or bad tagging conditions, however, one might expect that the residuals for males and females in a particular tagging episode would be similar for animals released at the same time. When all residuals for a given tagging episode were examined, there did not appear to be consistently low or consistently high residuals.

Comparison of the residuals for combined patterns associated with sex (Table 6a), tagging events (e.g., all February tagging periods, Table 6b) and recapture periods (e.g., all tags returned during February–May fishing period, Table 6c) identified areas of improvement in model fit of the strong effort assumption model

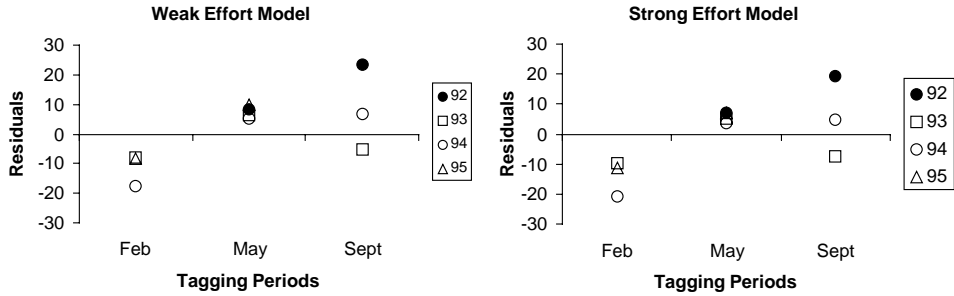
over the weak effort model. Although the total overall residual values for each sex were low for both models it appeared that the expected tag recoveries were generally underestimated for males and overestimated for females based on the weak effort assumption model (Table 6a). The residuals for both sexes were substantially reduced when expected recoveries were based on the model using the strong effort assumption. This indicates that incorporation of actual (rather than relative) effort improved the model fit for both males and females.

Improvements in modelling the data using the strong effort assumption produced mixed results when the combined tagging periods were taken into account (Table 6b). Improvements in model fit were observed for both sexes for September tagging periods and for males for May tagging period. There was an increase in the summed value of the residuals (poorer model fit) for the February tagging periods for both sexes and for females for the May tagging periods.

The overestimation of the expected recoveries for males for the February tagging periods and the underestimation during the other tagging periods for males suggest that there may be a biological effect associated with the time of tagging (Fig. 5). Such an effect could be associated with a change in tag-induced mortality associated with the timing of tagging. For example, pre-, post- or inter-moult lobsters may have different tag-induced mortality rates. The moulting period for males and females is September/October and May/June, respectively. The residuals show that there was considerable variation in the number of tags returned from tagging during the respective moulting periods. This could represent seasonal variation in the timing of the moult and an impact of tagging during this period. Cooler water temperatures may result in less bacterial infection and thus less tag-induced mortality or cooler water temperatures and lower metabolism could result in a greater time for recovery from tagging between feeding excursions.

Examination of the residuals for the recapture periods showed that the expected tag returns were generally underestimated for the September–February recapture period and overestimated for the February–May recapture period for the model based on the weak effort assumption (Table 6c). These were relatively even between sexes for the September to February period although females tended to be overestimated

Males



Females

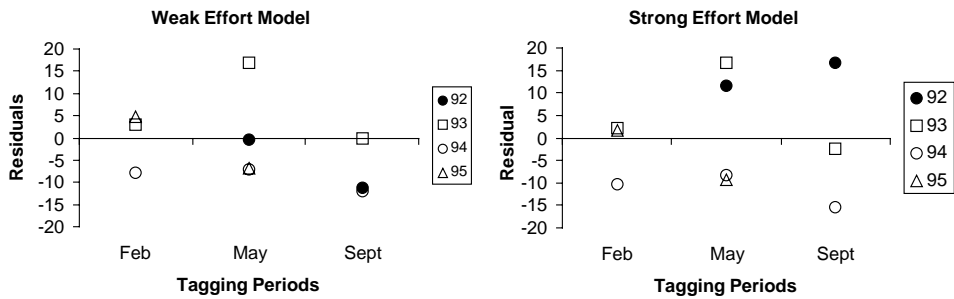
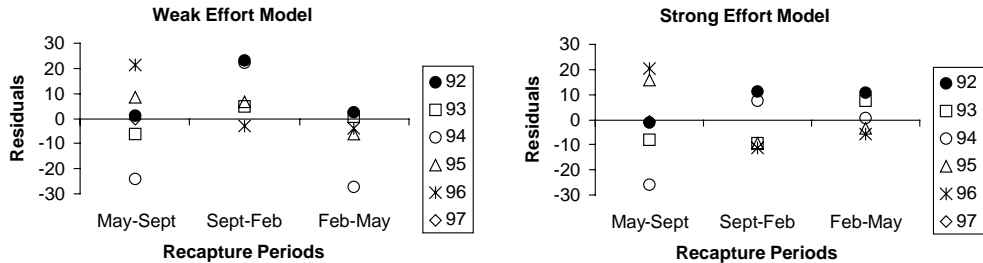


Fig. 5. Comparison of residuals between the weak and strong effort assumption models for males and females for the February, May and September tagging periods from May 1992 to 1995.

Males



Females

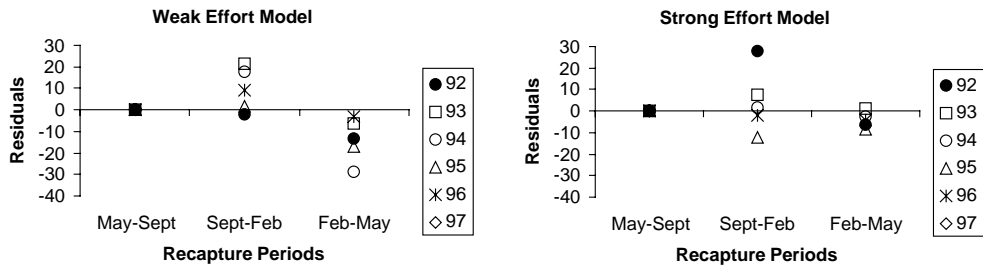


Fig. 6. Comparison of residuals between the weak and strong effort assumption models for the May–September, September–February and February–May tag-recapture periods from 1992 to 1997.

more than males for the February–May period. Incorporating absolute effort into the model resulted in a substantial improvement in the residuals for both sexes for both the September–February and February–May tag recovery periods (Fig. 6).

Ziegler et al. (2002) found substantial differences in catchability of lobsters throughout the fishing season and that these also varied with sex. Catchability of both sexes was higher during the Austral summer and declined with cooler waters during winter. Both sexes showed reduced catchability during the moulting period with males moulting in September/October and females in May. The underestimation of males by the weak effort assumption model during the September–February period is associated with the period of highest catchability when the fishery is open from November to February. Similarly the overestimation of tag recoveries for the February–May period by the weak effort assumption model is associated with declining catchabilities as the fishing season heads into winter. The greater overestimation in females is possibly due to females preparing to moult and mate during this period. The improvement in the residuals for the recapture periods in the strong effort assumption model indicates that the absolute effort being expended in each of the fishing periods between fishing years captures more of the dynamics of the fishery than proportioning effort within a year.

The lack of support for a model with catchability estimated separately for each sex is surprising as Frusher and Hoenig (2001b) found differences in trap selectivity with sex and Ziegler et al. (2002) found moulting, which occurs at different times for males and females, to influence catchability. This lack of improvement in model suggests that seasonal effects that influence both sexes equally, such as water temperature and mating, have the strongest impact on catchability.

4. Conclusion

We believe that incorporating the strong effort assumption into a multi-year tagging model with tagging events occurring within the fishing season can capture more of the biological reality of the lobster population under study and provide improved estimates of natural mortality and of fishing mortality after the cessation

of tagging. The approach is flexible enough to provide for catchability varying by sex, period of recapture, or other factors. The model provides greater parsimony by estimating fewer parameters than models based on the weak effort assumption. It appears the strong effort assumption model had fewer problems with patterns in the residuals than the weak effort assumption model. Both fishing mortality and tag reporting rate estimates were relatively insensitive to the way fishing effort was incorporated into the model. However, if catchability does not vary from year to year, annual estimates of fishing mortality can be obtained beyond the tag-recapture years if seasonal fishing effort values are known.

This paper has demonstrated that tagging models that incorporate several tagging events within a fishing year have the potential to estimate seasonal catchability coefficients in addition to estimates of the fishing mortality and natural mortality. All these parameters are important for assessing fish stocks.

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