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research paper

Accurate estimates of tag-induced mortality rates are contingent on the number of tagged and recaptured lobsters

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ABSTRACT.—Tag-induced mortality (TIM) biases many capture-recapture studies, leading to abnormally high mortality estimates in the first-year post-tagging. Although models exist to account for this bias, estimating TIM has been problematic and restricted to artificial environments. Here, we use a method for estimating *Jasus edwardsii* (Hutton, 1875) TIM in situ and demonstrate the conditions under which accurate estimates can be achieved. We use a long-term capture-mark-recapture study conducted since 2000 at the Crayfish Point Scientific Reserve (CPSR), Hobart, Tasmania, Australia, to estimate the rate of in situ tag induced mortality and demonstrate the assumptions relating to sampling design that are required to achieve accurate estimates. TIM estimates were high and relatively similar for both males and females. The similarity between sexes would indicate that for this species, combined sex estimates may be sufficient, which requires substantially less effort. Estimates of TIM were sensitive to the number of recaptured lobsters and at least 15 lobsters, tagged in an initial survey, had to be captured in two subsequent surveys. As recapture rates for lobsters over two subsequent recapture events are relatively low, this resulted in a large number of lobsters needing to be tagged in the initial survey. Given that most tagging studies have at least three surveys, we suggest that the design incorporate the ability to also estimate TIM. This is particularly important if tagging studies are used to estimate population parameters for exploited species, as not accounting for TIM would lead to overestimation of resources and inappropriate catch allocations.

Capture-mark-recapture (CMR) methods are commonly used for estimating demographic characteristics of crustaceans in the wild, including survival probability, population size, and migration, provided the tags can be retained over a series of molts (Pollock et al. 1990, Comeau and Mallet 2003, Frusher et al. 2009). In an open population, where it is not possible to separate natural mortality (death) and permanent migration, the Cormack-Jolly-Seber (CJS) model is used to estimate apparent survival probability.

Assumptions of CMR methods are outlined below and violation of these may lead to bias in CMR estimates (Pollock et al. 1990, 2007). These include:

(1) An equal probability of capture for every individual in the population at each sampling event. Biases in population estimates will occur if tagged and non-tagged animals do not mix freely and uniformly after tagging. Biases in estimates of survival probability will also occur if different tagging cohorts do not mix freely with each other.
(2) An equal probability of survival for every marked animal from one survey event to the next, irrespective of when it was tagged.
(3) Tag loss is zero or negligible. By decreasing the number of animals available to be recaptured in the population, tag loss can result in serious under-estimation (negative bias) of survival rates (Pollock et al. 1990) and over-estimation (positive bias) of population size (McDonald et al. 2003, Pollock and Alpizar Jara 2010).
(4) After sampling, all animals are released immediately back to the location of capture and the sampling period is of short duration compared to the period between successive tagging events. Recapture rate may be affected if the tagged animals are held for longer periods before release (Courtney et al. 2001).
(5) Emigration is permanent. Temporary emigration may lead to biased survival probability and population size estimates.

In any tagging study, the effect of tag loss and tag induced mortality (TIM) should be investigated as both result in fewer tagged animals being available for recapture and will therefore bias estimation of population parameters. TIM is defined as the death of a tagged animal due to factors either directly or indirectly related to the tagging process, including stress caused by capture, handling by the tagger, tag wounds, infection of the tagging area, and predation, as a result of capture and tagging. Additionally, TIM may vary with traits or biological aspects of tagged animals, such as molt stage or size. In lobsters, various studies have demonstrated that the most appropriate period of the molt cycle for tagging to minimize tag loss and tag induced mortality is during the inter-molt stage (Montgomery et al. 1995, Moriyasu et al. 1995, Frusher et al. 2009).

Determination of TIM rate, tag loss rate, and tag-related injuries has traditionally been estimated in aquaria facilities or with caging studies conducted in the field (Montgomery and Brett 1996, Davis et al. 2004, Dubula et al. 2005, Mattei et al. 2011, Gonzalez-Vicente et al. 2012). Unfortunately, aquaria-based studies of TIM can provide biased values as the artificial environment can place additional stress on captured animals and these environments also fail to replicate interactions with predators, prey, and habitat. In addition, aquarium studies usually comprise small sample sizes (Mattei et al. 2011) and/or short time periods (Montgomery and Brett 1996, Claverie and Smith 2007).

By contrast, in situ measurements of TIM can overcome several of the biases associated with aquarium or caged studies. To evaluate natural TIM for rock lobsters, Frusher et al. (2009) developed a model based on three survey events undertaken annually in the same location (Appendix 1). In survey one, lobsters were tagged and released. In survey two, captured lobsters comprised both lobsters that were tagged in survey one and untagged lobsters. All untagged lobsters were tagged and released along with the previously tagged lobsters. In survey three, captured lobsters included lobsters tagged in either the first survey or second survey and untagged lobsters.

Using this survey design, two questions were addressed in the present study. First, we compared two groups of lobsters from the surveyed population to estimate TIM. Group one comprised of lobsters tagged in the second survey and recaptured in the third survey. Group two comprised lobsters that were tagged in the first survey, recaptured in the second survey, and recaptured again in the third survey. The method is developed to estimate the initial impact of tagging by comparing group one recaptures that are impacted by tagging between surveys two and three to group two recaptures that experience the initial impact of tagging between survey one and two, and not between survey two and three. The timing of surveys dictates the period over which the impact of tagging is considered. In addition, as this method compares between two groups from the same population in the same location, natural mortality and other issues, such as migration, are expected to affect both groups equally.

Second, a drawback of the TIM modelling approach is that animals must be recaptured on two subsequent occasions, which can result in small data sets when tag return rates are low. Recognizing that CMR studies are expensive and there is a trade-off between effort and the precision of estimates, it is desirable to determine what sample size and sampling effort is required to gain reasonable estimates of TIM rate in the wild. In the present study, CMR data collected over 13 yrs (2000–2012) were used to estimate TIM rates in the wild for the southern rock lobster, *Jasus edwardsii* (Hutton, 1875), and to examine how varying numbers and size ranges of initially tagged lobsters affected estimates of TIM.

Methods

Study Area

Data collection occurred in the Crayfish Point Scientific Reserve (CPSR), near Hobart, Tasmania, Australia (42°57′08″S, 142°21′20″E; Fig. 1). This scientific reserve contains rocky reef habitat and is surrounded by sand, which limits rock lobster movement (Barrett et al. 2009). The reserve contains a temperate rocky reef of 1.24 km^2 with maximum depth of 15 m. Fishing for lobsters in the reserve has been banned since November 1971 and the reserve now holds a dense population of southern rock lobsters (Green et al. 2009).

Field Method

Annual tagging and recapture surveys have been conducted in the CPSR from 2000 to 2012 to support a range of research projects. The objectives for many of the projects varied resulting in considerable variation in the number of days that sampling was undertaken in each survey, the number of traps used each day and the number of lobsters captured and tagged. We focused on data from surveys undertaken approximately annually in November, December, January, and/or February, during the inter-molt period for both males and females, and when catchability is high (Ziegler et al. 2003). Trapping protocol followed the following procedures across all data sets; on the first day, traps were baited and set in the early afternoon. On subsequent days, the traps were checked in the morning, rebaited, and re-set. In all surveys,

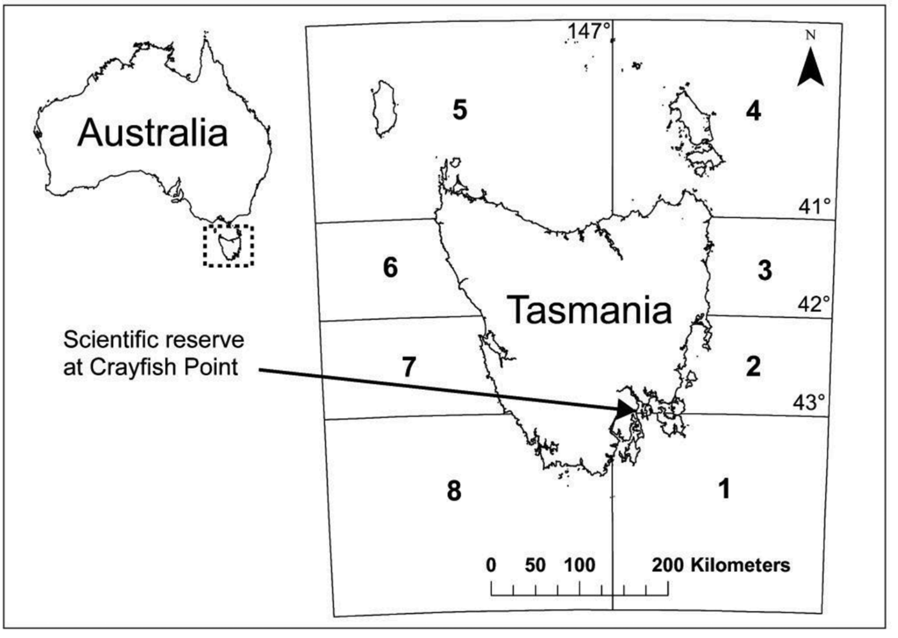

Figure 1. Map of study area investigating tag-induced mortality in *Jasus edwardsii*. Numbers 1 to 8 indicate fishing area around Tasmania, Australia.

bait and trap type were consistent. All untagged lobsters were tagged by a uniquely coded T-bar tag (Hallprint T-bar anchor tag; TBA1, Hallprint Pty Ltd, 27 Jacobsen Crescent, Holden Hill, South Australia 5088, Australia) on the ventral side of the first or second abdominal segment. The tag number, length of carapace, and sex of all lobsters were recorded and lobsters were released immediately after tagging.

The population of lobsters in the CPSR is only affected by natural mortality, as removal of tagged lobsters from the resource from fishing was not an issue, and emigration from the area was also considered minimal as southern rock lobster has high site fidelity (Barrett et al. 2009).

In November 2005, 1998 *J. edwardsii* (565 males and 1433 females) were translocated from Maatsuyker Island (south of Tasmania) and moved north to the CPSR. At capture, these lobsters were tagged with a uniquely coded T-bar tag prior to translocation. It was possible that these translocated lobsters had different behavioral or physical features that could have impacted the analyses in our study. We assume that the behavioral, physical, and physiological features of Maatsuyker Island and CPSR lobsters are similar enough to not impact the main focus of our findings.

Estimating Tag Induced Mortality (TIM) Rate

A 3-yr tagging model (Fig. 2, Appendix 1) developed by Frusher et al. (2009) was used to estimate TIM. Conceptually, the 3-yr model estimates survivorship between the first and second sampling events independently from that of the second and third sampling events. Additionally, survivorship is estimated separately for newly-tagged vs previously-tagged individuals. As tagging surveys were undertaken annually, the TIM estimates are the annual rate of lobsters that died from tagging during the year following being tagged.

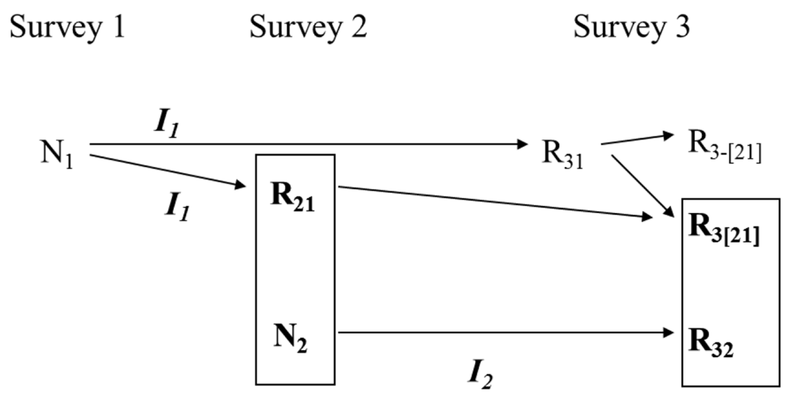

Figure 2. Three-year tagging survey method for estimating tag-induced morality (TIM) rates in *Jasus edwardsii*. The bold and boxed texts indicate the data used (from Frusher et al. 2009). The number of untagged lobsters captured and tagged on the first surveys are denoted N_1. Lobsters captured and tagged on the second survey are denoted N_2. Lobsters from N_1 that were recaptured and returned in the second capture period are denoted $R_{[21]}$. Lobsters caught in the third survey from the first survey are ($R_{[31]}$). $R_{[31]}$ comprises lobsters that were tagged in survey one and seen for the first time in survey three ($R_{3\text{-}[21]}$) and lobsters that were also seen in survey two ($R_{3[21]}$). I_1 and I_2 denote the impact of tagging on mortality of lobsters tagged in the first and second tagging surveys, respectively. It was assumed that no TIM occurs for these lobsters between the second and third surveys that were tagged in the first survey.

Estimation of TIM in the 3-yr model relies on keeping track of the numbers of previously- and newly-tagged lobsters in each year, and involves a few assumptions. First, TIM only occurs in the first year post-tagging, and that there are no residual impacts of tagging beyond the first year. Second, all lobsters are assumed to have equal catchability regardless of tagging status. Third, the differential mortality between newly-tagged and previously-tagged individuals is assumed to be due to TIM. Fourth, this model additionally assumes that no tagged lobsters are lost to migration, that tagged lobsters from each tagging event mix evenly with each other, and lastly, that each tagged lobster has an equal probability of being captured and/or recaptured, irrespective of when it was tagged for every individual in the population at each sampling event.

Most CMR analyses hinge on estimating capture probabilities to estimate survival. However, if capture probabilities are assumed to be equal across individuals and over time, and natural and tag induced mortality rates are assumed to be multiplicative, then estimation of TIM can proceed without calculating these rates. Instead, TIM for the period between survey two and three (I_2) is calculated as:

$$I_2 = 1 - \left(\frac{R_{[32]} * R_{[21]}}{R_{3[21]} * N_2} \right), \quad \text{(Eq. 1)}$$

where I_2 = tag induced mortality (TIM) rate for the period between survey two and three, $R_{[21]}$ = number of tagged lobsters captured in the second survey that were tagged in the first survey, $R_{[32]}$ = number of tagged lobsters captured in the third survey that were tagged in the second survey, $R_{3[21]}$ = number of tagged lobsters captured in the third survey that were tagged in the first survey and also captured in the second survey, and N_2 = number of lobsters tagged in the second survey.

Table 1. Design of 10 3-yr surveys for estimating tag-induced mortality (TIM). T = tagging event, R = recapture event, T/R = both tagging and recapturing events.

Surveys used for TIM estimation	Approximately annual tagging and recapture events											
	Nov 2000	Dec 2001	Jan–Feb 2003	Jan–Feb 2004	Jan 2005	Jan–Feb 2006	Jan 2007	Jan 2008	Feb 2009	Jan 2010	Jan 2011	Feb 2012
1	T	T/R	R									
2		T	T/R	R								
3			T	T/R	R							
4				T	T/R	R						
…												
9									T	T/R	R	
10										T	T/R	R

We used 12 approximately annual tagging and recapture data from 2000 to 2012, including three approximately annual (in November 2000, December 2001, and January–February 2003) and nine exactly annual tagging and recapture events (from January–February 2003 onwards), to set 10 3-yr periods for estimating TIM (Table 1), where the initial tagging event was followed by two additional years of recapture/tagging. For example, the initial tagging event in November 2000 was followed by a tagging/recapture event in December 2001, and a recapture event in January–February 2003.

Criteria for Determining TIM

Determination of Size Frequency of Tagged Lobsters.—The robustness of survival rate estimates in CMR studies increases with sample size (Lindberg and Walker 2007), which supports using the entire tagged population in each survey. However, we considered it plausible that TIM estimates were size dependent and there may be a benefit in restricting the size of animals included in the data set used for estimating TIM. This was explored by calculating TIM for data sets drawn from different size ranges. Males were larger than females in the CPSR; the most frequent 10 mm carapace length (CL) size bin was 121–130 mm CL and 101–110 mm CL for males and females, respectively from 2000 to 2012 (Fig. 3). Lobsters within this size bin were used as the smallest sample and this was incrementally increased by expanding the size bin width by 5 mm CL on either side. For example, male TIM was estimated for size bins 121–130, 116–135, 111–140 mm CL, etc., and female TIM was estimated for size bins 101–110, 96–115, 91–120 mm CL, etc.

Determination of Size Bin.—Accuracy of TIM estimates are affected by sample size, which is most problematic with the $R_{3[21]}$ group as this requires lobsters to be recaptured on two separate occasions.

To select the size bin with the highest numbers of tagged and recaptured lobsters ($R_{3[21]}$ and $R_{[32]}$), the relationships between size bin width and $R_{3[21]}$ and $R_{[32]}$ were separately evaluated. This relationship demonstrated how the number of tagged and recaptured lobsters would change with size bin width.

Determination of the Minimum Number of Recaptured Lobsters.—The minimum number of recaptured lobsters required to estimate TIM was estimated by calculating delta TIM (ΔTIM). This was defined as the change in the estimated TIM between successive size bin widths in every survey (Equation 2) and used to (1) determine the

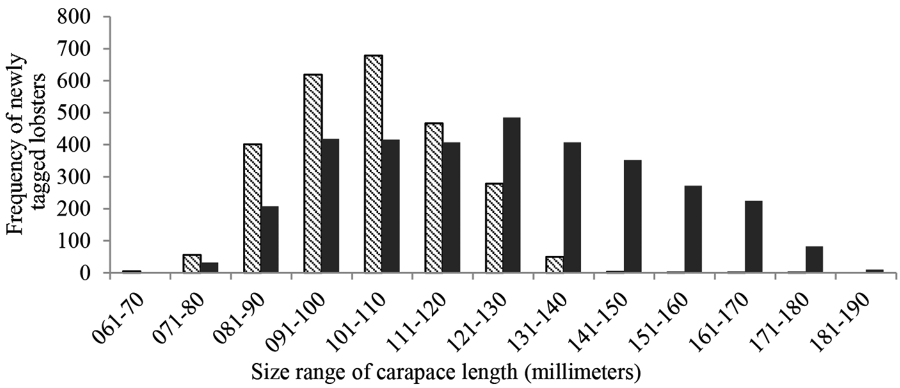

Figure 3. Size frequency of male (black column) and female (dashed column) lobsters, *Jasus edwardsii,* tagged from 2000 to 2012.

accuracy of the TIM estimates, and (2) find the minimum number of recaptured lobsters in the third survey ($R_{3[21]}$ and $R_{[32]}$) that resulted in accurate estimates. The accuracy of TIM estimates from these data sets with restricted size bins was considered high when estimates were within ±0.1.

$$\Delta TIM = TIM_{(n)} - TIM_{(n-x)}, \quad \text{(Eq. 2)}$$

where *n* refers to the smaller of two size bins and *x* refers to the sequential expansion of the size bins based on the chosen size increment. For example, for males where *n* = 121–130, *n*-1 = 116–135, *n*-2 = 111–140.

Confidence Interval for Estimated TIM.—Subsampling was used to investigate the standard error and confidence interval for the estimates of TIM. Only surveys undertaken in 2000, 2001, 2003, 2005, and 2006 (only for male lobsters) had more than 200 tagged male and female lobsters. From these surveys, groups of 200 newly tagged lobsters from the first tagging event of every three-survey data set were subsampled randomly with no replacement from the size bin of 96–155 for males and 81–130 for females with the statistical package R (R core team 2013).

In addition, subsamples with no replacement were taken of lobsters tagged in the second survey equal to the number of recaptured lobsters in the second survey, $R_{[21]}$. As $N_2 = R_{[21]}$, these two parameters cancelled each other out and TIM reduced to the following equation:

$$TIM = 1 - (R_{[32]}/R_{3[21]}). \quad \text{(Eq. 3)}$$

This process was repeated 50 times by 50 independent subsamples for sample size 200. We estimated SE for these 50 independent subsample. Then we used SE to estimate confidence interval (CI = Mean ± SE * 1.96).

Determination of Required Sample Size and Effort.—The main restriction for estimating TIM in the wild is the number of lobsters recaptured over two consequent recapture events. The number of lobsters recaptured in the third survey (second recaptured event) will depend on the number of tagged lobster (N_i), the number of tagged lobsters in the second survey ($R_{[21]}$), and the number of lobsters that were tagged in the first tagging event and recaptured in both the second and third surveys ($R_{3[21]}$).

To determine the number of lobsters that must be tagged in survey one to provide sufficient recaptures in survey three, we estimated the recapture probabilities of lobsters (β_i) for each survey.

Recapture probability of lobsters in survey three, ($\beta_{3[21]}$), from lobsters tagged in survey one and recaptured in survey two ($R_{[21]}$), is

$$\beta_{3[21]} = \frac{R_{3[21]}}{R_{[21]}}. \tag{Eq. 4}$$

Similarly, the recapture probability of lobsters in the second survey ($\beta_{[21]}$) from lobsters tagged in survey 1 ($\hat{N}_1$) is

$$\beta_{[21]} = \frac{R_{[21]}}{\widehat{N_i}}, \tag{Eq. 5}$$

where $\hat{N}_i$ denote the estimated number of tagged lobsters needed in the first survey.

The number of lobsters required to be tagged in survey one to ensure a predefined number of recaptured lobsters in the $R_{3[21]}$ category can be estimated by rearranging Equations 4 and 5:

$$\widehat{N_i} = \frac{R_{3[21]}}{\beta_{[21]} * \beta_{3[21]}}. \tag{Eq. 6}$$

The effort required to catch the estimated number of lobsters ($\hat{N}_i$) was calculated using the catch rate (number per trap lift) value from the first survey in each analysis of TIM. The catch rate for survey *i* (C_{ri}) was calculated from the observed number of lobster caught (N_i) and the number of traps deployed and hauled (T_i):

$$C_{ri} = {}^{N_i}\!/_{T_i}. \tag{Eq. 7}$$

For the first survey, N_1 is the total number of the tagged lobsters, while in the second and third surveys, N_2 and N_3 are the number of recaptured lobsters (equivalent to $=R_{[21]}$) and the number of lobsters recaptured over two consecutive surveys (equivalent to $=R_{3[21]}$), respectively.

The number of traps ($\hat{T}_i$) was estimated by:

$$\widehat{T_i} = \widehat{N_i}/C_{ri}. \tag{Eq. 8}$$

Table 2. Comparison of the number of recaptured lobsters in the third tagging event for increasing size bin widths for the three survey periods November 2000 (1st survey), December 2001 (2nd survey), and January/February 2003 (*see* Table 1). $R_{3[21]}$ denotes number of lobsters recaptured over two subsequent recapture surveys (i.e., lobsters tagged in the 1st survey and recapture in both 2nd and 3rd surveys, and $R_{[32]}$ denotes lobsters tagged in the 2nd survey and recaptured in the 3rd survey (the survey that we have only a recapture event and not a tagging event). * Size bins for males: 10 (121–130), 20 (116–135), 30 (111–140), etc., and for females: 10 (101–110), 20 (96–115), 30 (91–120), etc.

			Size bin widths (mm)*								
Tagging	Recaptures	Sex	10	20	30	40	50	60	70	80	90
Nov 2000	$R_{3[21]}$	Male	4	9	13	18	21	24	25	29	30
		Female	5	10	12	18	21	21	21	-	-
Dec 2001	$R_{[32]}$	Male	9	19	28	37	50	55	59	63	67
		Female	12	26	37	43	48	51	51	-	-

Results

The number of recaptured lobsters included in the data set was greater in wider size bins. For example, the number of recaptured lobsters at $R_{3[21]}$ and $R_{[32]}$ for different size bin widths associated with first and second tagging event undertaken in November 2000 and December 2001 highlights this trend (Table 2). Not surprisingly, recaptures that require two previous capture events ($R_{3[21]}$) have substantially fewer lobsters per size bin, which acts as a bottleneck in providing accurate estimates of TIM.

The Effect of the Numbers of Recaptures and Effort on TIM

The accuracy of the estimated TIM rate increased with the number of recaptured lobsters in the third survey (i.e., $R_{3[21]}$ and $R_{[32]}$). The number of $R_{3[21]}$ and $R_{[32]}$ required to obtain accurate estimates was at least 15 and 40 recaptured lobsters, respectively, where TIM estimates were within ±0.1 (Fig. 4; dashed line). From Table 2, this equates to size bin widths of at least 40 mm for males and females for $R_{3[21]}$, and 50 mm for males and 40 mm for females for $R_{[32]}$.

With lobsters from Maatsuyker Island (south of Tasmania) that have been translocated to the study area in November 2005, capture rates after this perturbation may not reflect the normal situation. Therefore, only three data sets spanning the required three survey were available for assessing required effort for accurate estimates of TIM (i.e., studies that started in November 2000, December 2001, and January–February 2003).

These data sets were used to estimate the sample size and effort required so that 15 lobsters would be required in survey three ($R_{3[21]}$) as determined in the previous section. Only surveys in November 2000, January–February 2003, and January 2005 met criteria of >15 lobsters in $R_{3[21]}$ and >40 lobsters in $R_{[32]}$. For females, only one initial sampling event (November 2000) resulted in sufficient recaptures in the third survey (Table 3), while this benchmark was achieved for males in three surveys. Females had substantially lower recapture rates than males, so more traps were required in each survey for successful estimation of female TIMs.

Across all surveys, using the mean number of lobsters recaptured and capture rates, the maximum number of traps required to produce an accurate estimate of

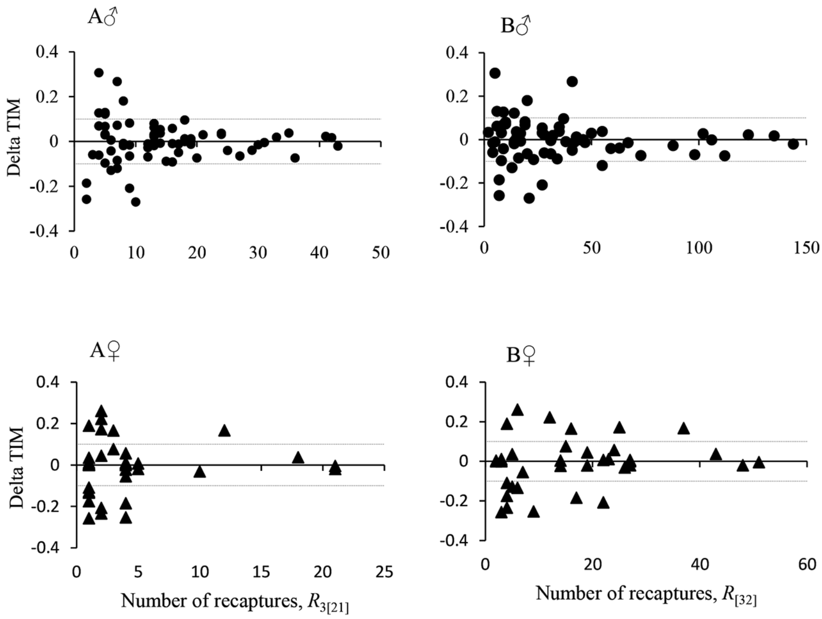

Figure 4. Accuracy of estimated tag-induced mortality (TIM) rates against the number of recaptured lobsters at (A) $R_{3[21]}$ and (B) $R_{[32]}$ for males (♂) and females (♀), separately. Dashed line shows delta TIM within ±0.1.

Table 3. Estimated and observed parameters required to obtain accurate TIM estimates for three-surveys. Bold indicates when the observed value was greater than the estimated. N_1 denotes the observed and/or estimated number of lobsters to be tagged in the first survey. T_1, T_2, and T_3 denote the number of traps set in the first, second, and third surveys, respectively.

	Males			Females			Combined sexes		
Sex/study parameters	Nov 2000	Dec 2001	Jan–Feb 2003	Nov 2000	Dec 2001	Jan–Feb 2003	Nov 2000	Dec 2001	Jan–Feb 2003
N_1									
Observed	**267**	**255**	**246**	**448**	393	228	**715**	**648**	**474**
Estimated	167	239	217	320	1,474	855	238	486	338
$R_{[21]}$									
Observed	**73**	**55**	**38**	**109**	48	14	**182**	**103**	**52**
Estimated	46	52	33	78	180	52	61	77	37
$R_{3[21]}$									
Observed	**24**	**16**	**17**	**21**	4	4	**45**	**20**	**21**
Fixed	15	15	15	15	15	15	15	15	15
T_1									
Observed	**891**	**602**	**801**	**891**	602	801	**891**	**602**	**801**
Estimated	557	564	707	636	2,257	3,004	297	451	572
T_2									
Observed	**602**	**801**	**403**	**602**	801	403	**602**	**801**	**403**
Estimated	376	751	356	430	3,004	1,511	201	601	288
T_3									
Observed	**801**	**403**	**708**	**801**	403	708	**801**	**403**	**708**
Estimated	501	378	625	572	1,511	2,655	267	302	506

Table 4. Comparison of the average (mean) number of observed (Obs) and estimated (Est) N_1, $R_{[21]}$, $R_{3[21]}$, Trap S_1, Trap S_2, Trap S_3 among three surveys (tagging event) started in November 2000, December 2001, and January–February 2003 for males, females, and combined sexes, respectively. N_1 = number and/or estimated number of lobsters to be tagged in the first survey, Cr = capture rate; Trap S_1, Trap S_2 and Trap S_3 = number of traps in survey 1, 2, and 3, respectively. The estimated number of lobsters in each survey is based on the minimum value of 15 lobsters to determine robust estimates of tag-induced mortality. Mean Cr (capture rate for observed parameters among three independent surveys started in November 2000, December 2001, and January–February 2003) was estimated by dividing the number of N_1, $R_{[21]}$, and $R_{3[21]}$ to the number of traps applied in the survey 1, 2, and 3 (i.e., Trap $_{S1}$, Trap $_{S2}$, Trap $_{S3}$), respectively, for males, females and combined sexes, separately.

	Males			Females			Combined sexes		
	Obs	Est	Mean Cr	Obs	Est	Mean Cr	Obs	Est	Mean Cr
N_1	256	197	0.34	356	563	0.48	612	305	0.82
$R_{[21]}$	55	42	0.09	57	80	0.09	112	53	0.19
$R_{3[21]}$	19	15	0.03	10	15	0.01	29	15	0.05
Trap $_{S1}$	765	572	-	765	1,173	-	765	371	-
Trap $_{S2}$	602	445	-	602	872	-	602	285	-
Trap $_{S3}$	637	480	-	637	1,077	-	637	332	-

TIM was 572 for males and 1173 for females (Table 4). The number of traps required to capture sufficient lobsters for an accurate estimate of TIM for combined sexes was 371.

Estimated Rates of TIM

From 2000 to 2012, there were only three occasions when TIM could be estimated accurately for males, one occasion for females, and five occasions for combined sexes. In these surveys, there were >15 and >40 recaptures of lobsters in categories $R_{3[21]}$ and $R_{[32]}$, respectively. Estimated TIM rate was lowest in 2005 (0.12) and highest in 2000 (0.34; Table 5). The average TIM rate for combined sexes was 0.35 (SD 0.06), and 0.25 (SD 0.12) and 0.37 for males and females, respectively (there was only a single estimate for females).

Estimates of TIM with subsampled data (200 subsamples with 50 replications) in the size bin of 95–155 (males) and 80–130 (females), as well confidence intervals (CI 95%) for these estimates, are presented in Table 5.

Discussion

Here we have shown how a model using data collected over three-surveys can be used to estimate tag induced mortality (TIM) rate of lobsters in the wild, as well as examining the sampling effort required to obtain accurate estimates. Traditionally, previous attempts to estimate annual TIM rates in lobsters have been reliant on aquaria studies or caging experiments (Montgomery and Brett 1996). A major benefit of this method is that TIM rates are estimated in situ by comparing tag returns from multiple tagging years. However, a weakness of the method is the need to recapture sufficient animals on two successive surveys. We found that at least 15 lobsters had to be recaptured in the third survey that were tagged in the first survey and also recaptured in the second survey ($R_{3[21]}$), and 40 lobsters needed to be captured that were tagged on the second survey ($R_{[32]}$). This minimum threshold for the number of

Table 5. Estimates of tag-induced mortality (TIM) rates with observed data for the size bins of 95–155 (males, M) and 80–130 (females, F). Overall TIM rate is mean with standard deviation. * Number of tagged lobsters in the first tagging event for every 3-yr survey. ** TIM rate was only estimated in four occasions for males, one occasion for females, and five occasions for combined sexes when $R_{3[21]} > 15$ and $R_{[32]} > 40$. *** Estimates of TIM with sub-sampled data (200 subsamples with 50 replications) in the size bin of 95–155 (males) and 80–130 (females). Inf = infinitive.

	Survey										
Variables by sex	Nov 2000	Dec 2001	Jan–Feb 2003	Jan–Feb 2004	Jan 2005	Jan–Feb 2006	Jan 2007	Jan 2008	Feb 2009	Jan 2010	Overall TIM
Sampling days											
M and F	10	7	11	7	10	12	7	4	4	4	
Traps											
M and F	891	602	801	403	708	885	419	232	239	240	
Tagged lobsters N_1*											
M	267	255	246	132	359	312	255	116	69	116	
F	488	393	228	143	363	191	156	91	56	90	
M and F	755	648	474	275	722	503	411	207	125	206	
Tagged lobsters N_2											
M	255	246	132	359	312	255	116	69	116	85	
F	393	228	143	363	191	156	91	56	90	34	
M and F	648	474	275	722	503	411	207	125	206	119	
Capture rate $\text{beta}_{3[21]} = R_{3[21]}/R_{[21]}$											
M	0.33	0.29	0.45	0.29	0.41	0.24	0.19	0.57	0.10	0.23	
F	0.19	0.08	0.29	0.15	0.23	0.04	0.00	0.00	0.33	0.50	
M and F	0.25	0.19	0.40	0.23	0.37	0.20	0.17	0.45	0.15	0.25	
Capture rate $\text{beta}_{[21]} = R_{[21]}/N_1$											
M	0.27	0.22	0.15	0.32	0.25	0.36	0.12	0.20	0.14	0.22	
F	0.22	0.12	0.06	0.19	0.06	0.14	0.03	0.07	0.05	0.02	
M and F	0.25	0.16	0.11	0.25	0.15	0.28	0.09	0.14	0.10	0.14	
Capture rate $\text{beta}_{[32]} = R_{[32]}/N_2$											
M	0.22	0.15	0.32	0.25	0.36	0.12	0.20	0.14	0.22	0.11	
F	0.12	0.06	0.19	0.06	0.14	0.03	0.07	0.05	0.02	0.09	
M and F	0.16	0.11	0.25	0.15	0.28	0.09	0.14	0.10	0.14	0.10	
Number of recaptured lobsters $R_{[21]}$											
M	73	55	38	42	88	112	31	23	10	26	
F	109	48	14	27	22	27	5	6	3	2	
M and F	182	103	52	69	110	139	36	29	13	28	
Number of recaptured lobsters $R_{3[21]} > 15$											
M	**24**	**16**	**17**	12	**36**	**27**	6	13	1	6	
F	**21**	4	4	4	5	1	0	0	1	1	
M&F	**45**	**20**	**21**	**16**	**41**	**28**	6	13	2	7	
Number of recaptured lobsters $R_{[32]} > 40$											
M	**55**	38	**42**	**88**	**112**	31	23	10	26	9	
F	**48**	14	27	22	27	5	6	3	2	3	
M and F	**103**	**52**	**69**	**110**	**139**	36	29	13	28	12	

Table 5. *Continued.*

	Survey										
Variables by sex	Nov 2000	Dec 2001	Jan–Feb 2003	Jan–Feb 2004	Jan 2005	Jan–Feb 2006	Jan 2007	Jan 2008	Feb 2009	Jan 2010	Overall TIM
TIM rate estimates**											
M	**0.34**	0.47	**0.29**	0.14	**0.12**	0.49	−0.02	0.74	−1.20	0.54	**0.25 (0.12)**
F	**0.37**	0.26	0.34	0.59	0.38	0.13	Inf	Inf	0.93	0.83	**0.37**
M and F	**0.36**	**0.44**	**0.38**	**0.34**	**0.26**	0.57	0.16	0.77	0.12	0.59	**0.35 (0.06)**
Estimated TIM (sub-sampled)***											
M	**0.36**	0.51	**0.27**		**0.17**	0.50					
F	**0.39**	041	0.44		0.59						
Confidence interval (95%)											
M	**0.32–0.40**	0.46–0.55	**0.23–0.32**		**0.13–0.21**	0.45–0.54					
F	**0.22–0.56**	0.10–0.72	0.26–0.63		0.42–0.75						

lobsters was used to estimate the number of traps required to capture 15 lobsters in the third survey. Recapture rates of females were substantially lower than for males, which meant that greater sampling effort would be required for determining TIM rates for females. It was estimated that an average of 600 trap sets would be required for males, 1200 for females, and 400 for combined sexes. This aspect of the study highlights the sex-specific biology for rock lobster.

The average TIM rate for males in the year after release was estimated at 0.25 and varied from 0.12 in 2005 to 0.34 in 2000. This variation in TIM rate may be due to multiple factors, including differences in handling and tagging. In the present study, tagging was conducted by different people ranging from students with no prior experience to staff with many years of experience, which may have led to differences in stress and injury. For example, inappropriate handling can result in the loss of some appendages, including antenna or legs, which can affect foraging and defense against predators, and thus increased mortality rates (Herrnkind et al. 2001, Parsons and Eggleston 2005, Frisch and Hobbs 2011). Parsons and Eggleston (2005) described three factors that increase predation rate of released injured lobsters, all of which could contribute to TIM: (1) releasing a mixture of organic compounds (e.g., blood) that may attract predators, (2) reduction in the defensive capacity of injured lobsters, and (3) the loss of cooperative group defense by injured lobsters. In 2005, around 2000 individual lobsters (28% male, 72% female) were captured from elsewhere and translocated into the site as part of an unrelated research project. This acute change in the population occurred 3 mo before the first annual recapture survey in 2005 and may have contributed to the extremely low estimate of TIM in 2005. Excluding this value from the overall male estimate provides an average of 0.315, which is closer to the overall female estimate. The only period when both male and female estimates were obtained from the same set of surveys also found little difference between male (0.34) and female (0.36) TIM estimates, suggesting that it would be appropriate to use data from both sexes combined. However, there may be other reasons for collecting separate data from sexes, such as dominance hierarchies that appear to affect recapture probabilities (Frusher and Hoenig 2001). In our study, TIM rate could be estimated for combined sexes for five data sets, which gave consistent estimates with a mean of 0.35 and standard deviation of 0.06. The consistent values across different years suggests TIM rate could be estimated on a small number of occasions and applied for longer time periods. Estimating TIM rate with data aggregated across all surveys provided rates of 0.30, 0.42, and 0.39 from males, females, and combined sexes, respectively.

Studies using aquaria and cage methods have also reported high estimates of TIM rate. Montgomery and Brett (1996) reported that TIM occurred after 4 wks for *Sagmariasus* (*Jasus*) *verreauxi* (H. Milne-Edwards, 1851) tagged with T-anchor tags and held in aquaria, in which the rate of TIM was 0.45, although results were compounded by other stressors as mortality also occurred in controls. Dubula et al. (2005) found that the rate of TIM in *Jasus lalandii* (H. Milne-Edwards, 1837) was 0.27 and 0.46 in aquarium and sea-cage studies, respectively. They reported that the higher rate of TIM estimates in sea cages was due to cannibalism when lobsters molted. Claverie and Smith (2007) observed a high rate of TIM (0.48) over a 60-d study for the galatheid, *Munida rugosa* (Fabricius, 1775), and attributed this to infection. Both Dubula et al. (2005) and Claverie and Smith (2007) observed black necrotic tissue around the wound associated with tagging.

The consistently high values of TIM across different studies and methods suggest that TIM is an important factor that requires consideration in tagging research of crustaceans, such as in the estimation of survival probability or population size. Tagging studies typically assume that all animals tagged in a survey are equally available for recapture at the next survey with losses attributed to either natural or fishing mortality. With substantially fewer lobsters available for recapture due to TIM, survival probabilities and population estimates that do not account for TIM would be overestimated.

In designing surveys, it is important to ensure that effort can be maintained across all surveys. For example, in 2008 and 2009, surveys were reduced from 7 to 4 d to reduce cost. While 4 d provided sufficient lobsters for size structure analysis, there were insufficient lobsters captured to estimate TIM.

The present study highlights the need for TIM rates to be estimated as an essential part of tagging programs. We provide a method that can be incorporated into a standard tagging program. Large estimates of TIM, as found in this and other surveys, would result in estimates of population size that are biased upwards and could lead to over exploitation of stocks. Finally, the high TIM rates observed in this and other studies suggest that there is a significant mortality cost to the use of T-bar tags in lobsters—a factor that could significantly harm the pool of animals on which research is focused. We note that while other factors, such as trap-shyness or permanent emigration, may lead to an apparent increase in TIM, the model assumptions made here lead us to the conclusion that such high mortality rates may simply be an unacceptable additional source of mortality in cases where animal numbers are low in the first place. The large and healthy population of lobsters at CPSR means that recovery from tag-induced losses is virtually assured. However, other populations that are harvested may not similarly be able to absorb such additional stressors. We therefore highlight the importance of assessing TIM in wild-tagging studies and advocate a risk assessment in the case that TIM is unacceptably high.

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Appendix 1

Development of In Situ Tag-induced Mortality Model (From Frusher et al. 2009)

In a tagging program, the first survey captures untagged animals and the released lobsters include lobsters tagged during that survey. On subsequent surveys, the catch will include lobsters tagged on previous surveys as well as untagged lobsters that are subsequently tagged during this event. Released lobsters include a mix of previously tagged and newly tagged lobsters. If the initial impact of tagging occurs between surveys then tagged lobsters recaptured in any subsequent survey would have survived the impact of tagging. By comparing the fate of previously tagged lobsters against the fate of newly tagged lobsters on subsequent surveys, the difference should be the initial impact of tagging. A minimum of three surveys are required to estimate tag induced mortality and the following example illustrates the method:

During each of two surveys, we tag a number of animals. During the second survey (S_2), we would recapture animals tagged during the first survey (S_1), and during the third survey (S_3), we would recapture animals that were tagged during both the first (S_1) and second (S_2) surveys.

If we assume that initial tag loss and tag-induced mortality occurs shortly after tagging and before the following survey, then recaptures will be a function of the total number tagged, the initial impact of tagging (which includes both initial tag loss and initial tag-induced mortality), and the recapture rate.

$$r_{i+1,i} \propto N_i(1-\theta_{I_i})\theta_{R_{i+1}}, \qquad \text{(Eq. 1)}$$

where $r_{i+1,i}$ = expected recaptures during survey i + 1 from animals tagged during survey i, N_i = number of animals tagged during survey i, θ_{I_i} = probability that animals die from the initial impact of tagging during survey i, θ_{R_i} = probability of recapture during survey i (recapture rate)

For three surveys a tagging/recapture matrix can be establish as follows:

Survey 1 (S_1)	Survey 2 (S_2)	Survey 3 (S_3)
Tagging (N_1)	Recapture $r_{21} = N_1(1-\theta_{I_1})\theta_{R_2}$	Recapture $r_{31} = N_1(1-\theta_{I_1})\theta_{R_3}$
	Tagging (N_2)	$r_{32} = N_2(1-\theta_{I_2})\theta_{R_3}$

Recaptures during S_3 will also include recaptures of animals that were recaptured and released during S_2 from tagging event 1. This subset of recaptures can be stated as follows:

$$r_{3[21]} = r_{21}\theta_{R_3}. \qquad \text{(Eq. 2)}$$

Note that Equation 2 is similar to the other equations in the tagging/recapture matrix with the number recaptured and returned during survey 2 now becoming the number of tagged lobsters released (i.e., r_{21} replaces N_1 in the equation estimating r_{31}) and as these animals were previously tagged, the initially impact of tagging for this cohort has already occurred [i.e., $\theta_{I_i} = 0$ and therefore $(1-\theta_{I_i}) = 1$].

If we divide r_{32} by $r_{3[21]}$, it is possible to estimate the initial impact of tagging associated with tagging event 2 using:

$$\frac{r_{32}}{r_{3[21]}} = \frac{N_2(1-\theta_{I_2})\theta_{R_3}}{r_{21}\theta_{R_3}}. \qquad \text{(Eq. 3)}$$

If we assume that the probability of capturing a tagged animal in the population is equal for animals tagged during surveys 1 and 2, then θ_{R_3} cancels out θ_{I_2} and is the only unknown. Equation 3 can be rearranged to give

$$1-\theta_{I_2} = \frac{r_{32}r_{21}}{r_{3[21]}N_2} \qquad \text{(Eq. 4)}$$

and

$$\theta_{I_2} = 1-\frac{r_{32}r_{21}}{r_{3[21]}N_2}. \qquad \text{(Eq. 5)}$$

The following is a worked example.

Let the number of animals tagged be 100 and 200 for S_1 and S_2, respectively. The initial impact of tagging is 10% for S_1 and 20% for S_2, and the tag recovery rate is 30% in S_2 and 40% in S_3.

Thus, $N_1 = 100$, $N_2 = 200$, $\theta_{I_1} = 0.1$, $\theta_{I_2} = 0.2$, $\theta_{R_2} = 0.3$, and $\theta_{R_3} = 0.4$.

Using the tagging/recapture matrix above, we get:

Survey 1 (S_1)	Survey 2 (S_2)	Survey 3 (S_3)
Tagging $N_1 = 100$	Recapture $r_{21} = 100 \times (1-0.1) \times 0.3 = 27$	Recapture $r_{31} = 100 \times (1-0.1) \times 0.4 = 36$ and $r_{3[21]} = 27 \times 0.4 = 10.8$
	Tagging $N_2 = 200$	$r_{32} = 200 \times (1-0.2) \times 0.4 = 64$

From Equation 5 we can estimate:

$$\theta_{I_2} = 1-\frac{64 \times 27}{10.8 \times 200} = 0.2.$$

It is worthwhile noting that neither chronic tag loss nor natural mortality has been incorporated into the methodology. It is assumed that natural mortality would be equivalent for both groups between surveys and thus cancel out. If tag loss is chronic and linear, then tag loss would be equivalent for both groups and θ would be a measure of tag-induced mortality only.