Estimating the emigration rate of fish stocks from marine sanctuaries using tag-recovery data

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Abstract—A critical process in assessing the impact of marine sanctuaries on fish stocks is the movement of fish out into surrounding fished areas. A method is presented for estimating the yearly rate of emigration of animals from a protected ("no-take") zone. Movement rates for exploited populations are usually inferred from tag-recovery studies, where tagged individuals are released into the sea at known locations and their location of recapture is reported by fishermen. There are three drawbacks, however, with this method of estimating movement rates: 1) if animals are tagged and released into both protected and fished areas, movement rates will be overestimated if the prohibition on recapturing tagged fish later from within the protected area is not made explicit; 2) the times of recapture are random; and 3) an unknown proportion of tagged animals are recaptured but not reported back to researchers. An estimation method is proposed which addresses these three drawbacks of tag-recovery data. An analytic formula and an associated double-hypergeometric likelihood method were derived. These two estimators of emigration rate were applied to tag recoveries from southern rock lobsters (*Jasus edwardsii*) released into a sanctuary and into its surrounding fished area in South Australia.

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Marine sanctuaries, also known as marine protected areas (MPAs), marine reserves, and no-take areas, are being widely promoted and implemented. Important for assessing the impact of these "no-take" sanctuaries (from which fishing has been excluded) on exploited populations is the rate of emigration of animals out into the remaining fished habitat.

The most widely available data for estimating movement rates of commercially or recreationally exploited populations are those from tagged and recovered fish (Hilborn, 1990). Animals are captured alive, a visible numbered tag is inserted and they are released back into the wild. Because the accuracy of tag-recovery studies relies on fishermen reporting recaptured tags, the quality of tag-recovery information is lower than that from a controlled experiment.

Tag-recovery experiments have three limitations for estimating movement rates of animals—the first two apply to most tagged populations, the third applies specifically to emigration from sanctuaries: 1) times at large (the numbers of days from when each animal is tagged and released to when it is subsequently recaptured in the fishery) are highly variable; 2) not all recaptured tags are reported to researchers by fishermen and this rate of tag nonreporting is often unknown; and 3) tag recoveries cannot be obtained from within sanctuaries for the simple reason that no fishing is allowed there.

If this last asymmetry (of recaptures from the sanctuary coming only from tagged animals that emigrate) is not accounted for in the estimation model, then the emigration rate out of the sanctuary will be overestimated. With previous movement estimators, tag releases and recaptures from all strata have been assumed. The aim of the present article is to develop an unbiased estimator of emigration rate from no-take areas by using data of tag releases both into the sanctuary and into the fished zone surrounding it, but where recoveries from nonmoving tagged animals are only possible from the fished zone. An estimate for the recovery rate (proportion of fish recaptured and their tags reported) in the fished zone was also obtained.

Materials and methods

Tag-recovery data

The data used to estimate the emigration rate from Gleesons Landing Lobster Sanctuary (Fig. 1) are tag recoveries from lobsters tagged and released both inside the sanctuary and into the fished zone surrounding the sanctuary. A large South Australian lobster tagging program was undertaken in 1993–96 throughout South Australian waters. T-bar tags (Hallprint, Victor Harbour, South Australia) were inserted into the ventral muscle at the first segment of the lobster abdomen. The rate of tag shedding was estimated from double tags at between 6% and 12% per year (Xiao[1]) and is incorporated in the recovery rate.

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[1] Xiao Y. 2003. Personal commun. Aquatic Sciences, South Australian Research and Development Institute (SARDI), P.O. Box 120, Henley Beach, South Australia 5022, Australia.

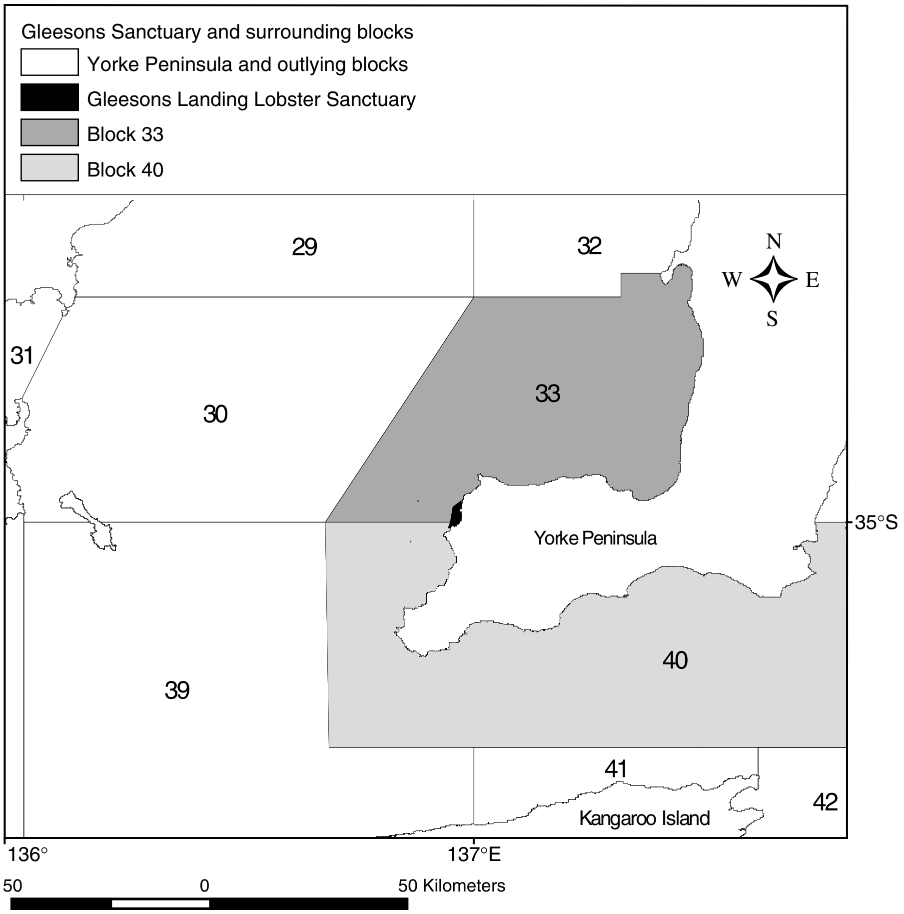

Figure 1

Location of Gleesons Landing Lobster Sanctuary (small dark area on the boundary of MFA blocks 33 and 40) along the west coast of the Yorke Peninsula in South Australia.

As part of this tagging program (Table 1), 3235 southern rock lobsters (*Jasus edwardsii*) were tagged and released into the "fished zone" surrounding Gleesons Sanctuary, namely into statistical reporting blocks 33 and 40 (Fig. 1). In January 1994, 413 lobsters were captured, tagged, and released inside the Gleesons Sanctuary. These lobsters were predominantly in the range of 80–120 mm carapace length (CL), around the size of maturity of about 100 mm CL; more lobsters below the legal minimum length (98.5 mm CL) were released in the fished zone.

Gleesons Landing Lobster Sanctuary (Fig. 1) is an area where lobster fishing has been prohibited since 1982. It lies along the Yorke Peninsula's western coast in an area of medium to low lobster catches. In width, this sanctuary extends 1–2 km from shore to seaward and runs 7–8 km north-south.

Nearly all tag recoveries were reported by commercial lobster fishermen who noticed tagged lobsters in their catch in the course of day-to-day fishing operations. Tag recoveries of lobsters released into both the sanctuary and the fished zone were, therefore, only possible from the fished zone. GPS coordinates, date, and carapace length were recorded for all tagged and recaptured lobsters. Longer-range movements from both sanctuary and fished zone were directed southwest towards the shelf edge.

Prescott et al.[2] previously described qualitative features of the movement of South Australian *Jasus edwardsii*: 1) nearly all longer-distance movements were directed offshore to deeper water and away from the coast; 2) in order of greater to lesser average distances moved, were i) immature females, ii) males, and iii) mature or egg-bearing females, for nearly all five South Australian regions analyzed; 3) movements were largely restricted to lobsters in a specific length range at time

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[2] Prescott, J., R. McGarvey, G. Ferguson, and M. Lorkin. 1998. Population dynamics of the southern rock in South Australian waters. Fisheries Research and Development Corporation of Australia Report 93/086, p. 23–27. Aquatic Sciences, South Australian Research and Development Institute (SARDI), P.O. Box 120, Henley Beach, South Australia 5022, Australia.

Table 1

Tag-recovery data from Gleesons Landing lobster sanctuary and the surrounding fishing zone used in estimating yearly movement rates of southern rock lobsters.

Data	Variable name	Observed number of lobsters
Number of lobsters tagged and released into the sanctuary	$\tilde{N}^S_T$	413
Number of lobsters recovered that had moved (≥3 km) from the sanctuary into the fishing zone	$\tilde{N}^S_{M,R}$	29
Number of lobsters tagged and released into the surrounding fishing zone	$\tilde{N}^F_T$	3235
Number of lobsters recovered that had moved (≥3 km) within the fishing zone	$\tilde{N}^F_{M,R}$	89
Number of lobsters ecovered that had not moved (≥3 km) within the fishing zone	$\tilde{N}^F_{NM,R}$	277

of tagging, roughly 100–140 mm CL for females, and 100–150 mm CL for males, with a noticeable shift to smaller sizes for both sexes on the southeast coast of South Australia where growth and thus size of maturity are known to be lower; 4) overall, most lobsters in the fished areas did not move large distances, about 15% moving more than 5 km; 5) two areas stood out as being habitats from where significant movement occurred, the coastal zone off the Coorong and Yorke Peninsula; and 6) for Yorke Peninsula, higher than proportional numbers of tagged lobsters that moved significant distances were tagged and released inside Gleesons Sanctuary.

In the present study study, a lobster was classified as having undergone movement if its measured distance from point of tagging to point of recapture was greater than 3 km. This definition of lobster "movement" was chosen for two reasons. 1) The mean width of MPA coastal zone to be protected in the currently proposed state representative system is assumed to be 5 km wide; that is, it is assumed that sanctuary areas will extend from the shore outward to sea across the full 3 nmi (which is about 5 km) of state territorial waters. Thus, a 3-km movement would represent slightly more than the mean distance needed for lobsters to leave the state-protected territorial waters of the reserve and enter waters open for fishing. This assumption is strengthened by the knowledge that most longer-range movements of South Australian rock lobster are directed from inshore to offshore. 2) According to the geographical features of the present study, a 3-km movement seaward from any location in Gleesons Landing Sanctuary would place the tagged lobster well into the fished zone, i.e., it would constitute a movement out of the sanctuary. Of sanctuary-tagged lobsters, 4 of 33 recaptured lobsters in the first season after tagging exited the reserve but moved less than 3 km. These 4 recaptured lobsters were excluded from the data set. The mean distance moved by lobsters from the sanctuary was 37.4 km.

Because movement of South Australian lobsters is directed strongly away from the inshore zone, the immigration rate of lobsters back into the Gleesons Landing Sanctuary is likely to be quite low. Moreover, *Jasus edwardsii* seek shelter daily and remain on specific reefs through most of their life (MacDiarmid et al. 1991; Kelly 2001). Long-distance movements occur rarely more than once in a lifetime. Thus, in the fishing zone, where there is a continual removal of adult lobsters from reef habitat, the on-going creation of new shelter space is higher than in the sanctuary and thus lobsters that did stray inshore into the sanctuary would be less likely to find shelter, further reducing the probability of migration into the sanctuary. In the estimator presented below, only the emigration rate (the movement rate out of the sanctuary) is calculated.

The recapture data included lobsters at large for a wide range of times, many having been recaptured longer than one year after tag release. However, to estimate emigration rate, we sought the proportion of lobsters emigrating out per year. Therefore, subsets of recapture data were selected that had a mean time at large of one year. The temporal distributions of recaptured lobsters showed distinct modes around 1 year at large (recaptures between 0.5 and 1.5 years at large, Fig. 2), and the number of recaptures in these 1-year modes were used for estimating yearly movement rate (Table 1).

Some tagged and released lobsters were recaptured more than once. For these lobsters, the single recapture was selected and used for which the time at large was closest to one full year.

Notation

The information on movement in each set of tag releases is taken to be binary: each recaptured animal is classified as having moved or as having not moved during its approximately 1-year time at large (from time of tag release to time of recapture).

To carry out the movement-rate estimation, it is useful to consider the complete set of four possible outcomes for each tagged and released animal: 1) it moved and was recovered after one year (denoted M,R); 2) it did not move and was recovered after one year (NM,R); 3) it moved and was not recovered after one year (M,NR); 4) it did not move and was not recovered after one year (NM,NR). These four possible recapture outcomes applied to animals tagged and released in both strata,

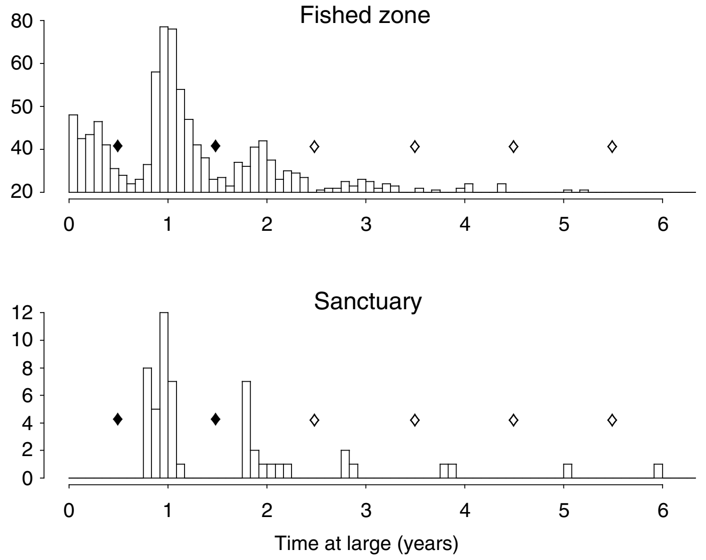

Figure 2

Histograms over time at large (in monthly bins) of recapture numbers from the fishing zone (MFA blocks 33 and 40) and from the Gleesons Landing Lobster Sanctuary. The diamond markers indicate divisions between modes at 0.5, 1.5., 2.5, etc. years at large; recaptures from the sanctuary and fishing zone that occurred between 0.5 and 1.5 years after release (between the black diamond markers) identify the subsets of data used to estimate yearly emigration rate from the sanctuary.

inside and outside the sanctuary. The tag-recovery data provided direct measures for only three of these eight possible numbers of recaptures.

We define "not recovered" to include both tagged animals that were not recaptured, as well as those that were recaptured by a fisherman but whose tag information (notably the location of recapture) was not reported back to researchers and therefore was not included in the tag-recovery database.

The movement-rate estimate is given in terms of the following data inputs: the number of lobsters tagged and released in 1) fished and 2) protected zones, and the numbers recovered that 3) moved (≥3 km) or 4) did not move from the fished zone over one year after tagging, and the 5) number that moved (≥3 km) from the sanctuary in one year.

Superscripts '*F*' and '*S*' denote fished zone and sanctuary, respectively, for the location of tag release. Let $N^F_{NM,R}$ and $N^F_{M,R}$ denote the numbers of animals that were recovered after a year and that moved or that did not move in the fished zone. From animals tagged and released inside the sanctuary, only the number that moved and were recovered ($N^S_{M,R}$) is available as an unbiased measure. In addition, we know the total number of animals originally tagged and released in the fished zone and sanctuary, N^F_T and N^S_T. Input quantities from the tag-recovery data set will henceforth be indicated by a tilde (˜): {$\tilde{N}^S_{M,R}, \tilde{N}^S_T, \tilde{N}^F_{NM,R}, \tilde{N}^F_{M,R}, \tilde{N}^F_T$} (Table 1).

Assumptions

Three assumptions were used to derive an emigration-rate estimate: 1) The two ways to define an estimate for the proportion that moved within the fished zone, namely as a proportion by using only recapture numbers, and as a proportion over the number originally tagged, can be set equal. 2) Recapture probabilities of animals that were tagged and released inside the sanctuary and that moved are assumed to equal those that were tagged and released into the fished zone and that also moved. (The first two assumptions were employed explicitly in steps 2 and 3 below.) 3) A third assumption is implicit in step 2, specifically in the recapture-conditioned movement proportion in the fished zone ($P^{F,R}_M$, Eq. 2): recapture probabilities of animals tagged and released in the fished zone that moved and of those that did not move are assumed to be equal. Assumptions 2 and 3 would both follow from assuming equal recapture probabilities for all lobsters in the fished zone.

Emigration rate: derivation of the estimate formula

In this section, an emigration-rate formula is derived. It provides a closed-form estimate of the yearly proportion of lobsters emigrating out of the sanctuary.

The proportion of animals moving can be estimated from tag-recovery data in two ways, namely as "tag-conditioned" and "recapture-conditioned" proportions. A tag-conditioned movement proportion (Eq. 1) is the total number of lobsters that moved (≥3 km) divided by the number originally tagged and released. It includes, in the numerator, all tagged animals that moved, both those that were recovered, as well as those that were not recovered. With a recapture-conditioned movement-rate estimate (e.g., Eq. 2), only counts of recaptured lobsters are used. The estimate expresses the movement proportion as the number of tagged animals that were recaptured and that also moved (≥3 km) divided by the total number recaptured. These two definitions for the movement proportion will be used to derive an estimation formula in terms of the five data inputs.

Step 1 The derivation begins by writing the estimate for proportion of lobsters that moved (P^S_M) in tag-conditioned form:

$$P^S_M = \frac{\tilde{N}^S_{M,R} + N^S_{M,NR}}{\tilde{N}^S_T}. \qquad (1)$$

This estimate of movement rate from the sanctuary is based on a tag-conditioned proportion because we have no observations of recaptured lobsters from the sanctuary that did not move (no unbiased measure of $N^S_{NM,R}$) which a recapture-conditioned movement proportion would have required. However we did have information about $N^S_{M,NR}$, the nonrecovery of tagged animals that emigrate from the sanctuary into the fished zone. It can be estimated (steps 2 and 3) with the second assumption that recovery rate for lobsters moving from the sanctuary equals that of lobsters moving (≥3 km) within the fished zone.

Step 2 Under assumption 1, the two ways in which movement proportion in the fished zone can be defined (as tag- and recapture-conditioned proportions) are equated. For fished zone releases, the recapture-conditioned ('*rc*') movement proportion is written

$$P^{F,rc}_M = \frac{\tilde{N}^F_{M,R}}{\tilde{N}^F_{NM,R} + \tilde{N}^F_{M,R}}. \qquad (2)$$

For the recapture-conditioned estimate formula (Eq. 2), all three quantities on the right-hand side are given as data inputs. With only numbers of lobsters recovered, the formula is, in this sense, conditional on recapture.

The tag-conditioned ('*tc*') proportion of lobsters moving ≥3 km of those released in the fished zone is written

$$P^{F,tc}_M = \frac{\tilde{N}^F_{M,R} + N^F_{M,NR}}{\tilde{N}^F_T}. \qquad (3)$$

The first assumption is

$$P^{F,rc}_M = P^{F,tc}_M. \qquad (4)$$

Substituting Equations 2 and 3 into Equation 4 and solving for $N^F_{M,NR}$, the number of lobsters that moved ≥3 km within the fished zone but were not recovered, yields

$$N^F_{M,NR} = \tilde{N}^F_{M,R}\left\{\frac{\tilde{N}^F_T}{\tilde{N}^F_{NM,R} + \tilde{N}^F_{M,R}} - 1\right\}. \qquad (5)$$

Step 3 Assumption 2 permits the derivation of a formula for $N^S_{M,NR}$. We first define the recovery proportions of animals that moved within the fished zone (F) as

$$f^F_M = \frac{\tilde{N}^F_{M,R}}{\tilde{N}^F_{M,NR} + \tilde{N}^F_{M,R}} \qquad (6)$$

and from the sanctuary (S) as

$$f^S_M = \frac{\tilde{N}^S_{M,R}}{N^S_{M,NR} + \tilde{N}^S_{M,R}}. \qquad (7)$$

Assumption 2, that the recovery rate (necessarily in the fished zone) for animals that were tagged and released in the sanctuary and that moved into the fished zone is the same as for animals that were both released and recaptured after moving within the fished zone becomes

$$f^F_M = f^S_M. \qquad (8)$$

Substituting Equations 6 and 7 into Equation 8 and rearranging terms, we have

$$N^S_{M,NR} = \frac{\tilde{N}^S_{M,R}\left(N^F_{M,NR} + \tilde{N}^F_{M,R}\right)}{\tilde{N}^F_{M,R}} - \tilde{N}^S_{M,R}. \qquad (9)$$

Step 4 Substituting Equation 5 into Equation 9 and substituting the result into Equation 1 yields a closed-form estimation formula for the quantity we seek, the proportion moving from the sanctuary in one year:

$$P^S_M = \frac{\tilde{N}^F_T \cdot \tilde{N}^S_{M,R}}{\tilde{N}^S_T \cdot (\tilde{N}^F_{NM,R} + \tilde{N}^F_{M,R})}. \qquad (10)$$

Numerical estimator: double-hypergeometric likelihood method

A likelihood formulation of this estimator was also constructed. The likelihood function describing a single tag-recapture experiment is hypergeometric (Seber, 1982; Rice, 1995) because sampling is without replacement. The set of possible outcomes from each of the two tagging experiments can be formulated as a 2×2 contingency table for the experimental populations of all lobsters originally tagged and released. The two pairs of outcomes represented in each contingency table are "moved" or "not moved" and "recovered" or "not recovered," yielding the four possible outcomes from both sets of tag releases (see "Notation" section).

In this study the data from two interacting tag-recovery experiments were used to generate an estimate of reserve emigration rate, namely of lobsters tagged and released into the sanctuary and into the fished zone. Thus, the product of a pair of linked hypergeometric probability mass functions, each corresponding to a 2-way contingency table, is the natural form of the likelihood function for P_M^S.

The derivation of Equation 10 was made with two assumptions, namely Equations 4 and 8. Incorporated in the likelihood, the two assumptions constrain the eight recapture numbers in the contingency tables. In the likelihood formulation, a third constraint was needed which is analogous to assumption 1 but which applies to sanctuary releases.

The derivation for constructing this likelihood from a pair of linked hypergeometric probability functions will proceed by 1) writing out the "raw" contingency tables in terms of the eight recapture numbers (N), as denoted in the "Tag-recovery data" and "Notation" sections, 2) algebraically re-expressing the elements of the tables so that the parameter to be estimated is explicit, 3) imposing the three constraints, and 4) writing out the likelihood, using the hypergeometric form for contingency tables.

For the lobsters tagged and released in the sanctuary, the raw contingency table is

	Recovered	Not recovered	Totals
Moved	$\tilde{N}^S_{M,R}$	$N^S_{M,NR}$	$\tilde{N}^S_{M,R} + N^S_{M,NR}$
Not moved	$N^S_{NM,R}$	$N^S_{NM,NR}$	$\tilde{N}^S_T - (\tilde{N}^S_{M,R} + N^S_{M,NR})$
Totals	$\tilde{N}^S_{M,R} + N^S_{NM,R}$	$\tilde{N}^S_T - (\tilde{N}^S_{M,R} + N^S_{NM,R})$	$\tilde{N}^S_T$

For the lobsters tagged in the fished zone:

	Recovered	Not recovered	Totals
Moved	$\tilde{N}^F_{M,R}$	$N^F_{M,NR}$	$\tilde{N}^F_{M,R} + N^F_{M,NR}$
Not moved	$\tilde{N}^F_{NM,R}$	$N^F_{NM,NR}$	$\tilde{N}^F_T - (\tilde{N}^F_{M,R} + N^F_{M,NR})$
Totals	$\tilde{N}^F_{M,R} + \tilde{N}^F_{NM,R}$	$\tilde{N}^F_T - (\tilde{N}^F_{M,R} + \tilde{N}^F_{NM,R})$	$\tilde{N}^F_T$

The two hypergeometric probability mass functions (pmfs) giving the model-predicted proportion of lobsters that moved and were recovered, based on the two contingency tables, are written as

$$P(\tilde{N}^S_{M,R}) = \left(\frac{\dbinom{\tilde{N}^S_{M,R} + N^S_{M,NR}}{\tilde{N}^S_{M,R}} \dbinom{\tilde{N}^S_T - (\tilde{N}^S_{M,R} + N^S_{M,NR})}{N^S_{NM,R}}}{\dbinom{\tilde{N}^S_T}{\tilde{N}^S_{M,R} + N^S_{NM,R}}} \right) \tag{11}$$

$$P(\tilde{N}^F_{M,R}) = \left(\frac{\dbinom{\tilde{N}^F_{M,R} + N^F_{M,NR}}{\tilde{N}^F_{M,R}} \dbinom{\tilde{N}^F_T - (\tilde{N}^F_{M,R} + N^F_{M,NR})}{\tilde{N}^F_{NM,R}}}{\dbinom{\tilde{N}^F_T}{\tilde{N}^F_{M,R} + \tilde{N}^F_{NM,R}}} \right). \tag{12}$$

Because the goal is to estimate the movement proportion, P_M^S (rather than any specific value of N), this proportion will need to be made explicit in the likelihood function as the sole freely varying parameter. Substituting from the definition of P_M^S (Eq. 1), we have

$$N^S_{M,NR} = P^S_M \cdot \tilde{N}^S_T - \tilde{N}^S_{M,R}. \tag{13}$$

Substituting for all occurrences of $N^S_{M,NR}$, Equation 11 becomes

$$P(\tilde{N}^S_{M,R}) = \left(\frac{\dbinom{P^S_M \cdot \tilde{N}^S_T}{\tilde{N}^S_{M,R}} \dbinom{\tilde{N}^S_T \cdot (1 - P^S_M)}{N^S_{NM,R}}}{\dbinom{\tilde{N}^S_T}{\tilde{N}^S_{M,R} + N^S_{NM,R}}} \right). \tag{14}$$

Writing the full joint-likelihood expression formed by the product of the two hypergeometric pmfs gives

$$L = \left(\frac{\dbinom{\tilde{N}^F_{M,R} + N^F_{M,NR}}{\tilde{N}^F_{M,R}} \dbinom{\tilde{N}^F_T - (\tilde{N}^F_{M,R} + N^F_{M,NR})}{\tilde{N}^F_{NM,R}}}{\dbinom{\tilde{N}^F_T}{\tilde{N}^F_{M,R} + \tilde{N}^F_{NM,R}}} \right) \times \left(\frac{\dbinom{P^S_M \cdot \tilde{N}^S_T}{\tilde{N}^S_{M,R}} \dbinom{\tilde{N}^S_T \cdot (1 - P^S_M)}{N^S_{NM,R}}}{\dbinom{\tilde{N}^S_T}{\tilde{N}^S_{M,R} + N^S_{NM,R}}} \right).$$

As formulated, the value of $N^S_{NM,R}$ is still undetermined by data or constraint. A third constraint is therefore required. As with assumption 1 for the fished zone (Eq. 4), we apply the assumed equivalence of tag- and recapture-conditioned proportions to the sanctuary releases:

$$P^{S,rc}_M = \tilde{N}^S_{M,R} / (N^S_{NM,R} + \tilde{N}^S_{M,R}) = P^{S,tc}_M = (\tilde{N}^S_{M,R} + N^S_{M,NR}) / \tilde{N}^S_T.$$

In this application, $N^S_{NM,R}$ is understood as the number of lobsters that would have been taken if fishing had not been excluded from the sanctuary. Solving for $N^S_{NM,R}$ yields the third constraint,

$$N^S_{NM,R} = (\tilde{N}^S_{M,R} \cdot \tilde{N}^S_T) / (\tilde{N}^S_{M,R} + N^S_{M,NR}) - \tilde{N}^S_{M,R},$$

Table 2

Intermediate calculated quantities from the numerical estimation. The equalities of $P_M^{F,rc}=P_M^{F,tc}$ and $f_M^F=f_M^S$ state assumptions 1 and 2.

Intermediate quantity	Variable name	Estimate
The proportions of lobsters tagged in the fishing zone that moved (≥3 km); recapture-conditioned ($P_M^{F,rc}$) or tag-conditioned ($P_M^{F,tc}$)	$P_M^{F,rc}=P_M^{F,tc}$	0.243
Number of lobsters that moved but were not recovered in the fishing zone	$N_{M,NR}^F$	697.7
Number of lobsters that moved from the sanctuary but were not recovered	$N_{M,NR}^S$	227.3
Number of lobsters that did not move and would have been recovered had there been equivalent levels of harvesting in the sanctuary	$N_{NM,R}^S$	17.7
Recovery proportions (in the fishing zone)—assumed to be equal for lobsters that moved inside the fishing zone f_M^F or from the sanctuary	$f_M^F=f_M^S$	0.113

without which this numerical estimator did not converge.

The factorial terms in the binomial coefficients of Equations 12 and 14 are defined only for natural numbers. However, in numerical minimization, factorials must be replaced with continuously varying approximations because the negative log-likelihood objective function is minimized by using numerical derivatives. The factorial z! was extended from natural numbers to the real line by using the gamma function, $\Gamma(z+1)$ and by using an asymptotic approximation formula for ln $\Gamma(z)$ (Eq. 6.1.41 in Abramowitz and Stegun, 1965):

$$\ln\Gamma(z)=\left(z-\frac{1}{2}\right)\ln(z)-z+\frac{1}{2}\ln(2\pi)+\frac{1}{12z}-\frac{1}{360z^3}+\frac{1}{1260z^5}-\frac{1}{1680z^7}+\frac{1}{1188z^9}-\frac{691}{360360z^{11}}+\frac{1}{156z^{13}}. \tag{15}$$

The negative log likelihood was minimized numerically by using the AD Model Builder parameter estimation software (http://otter-rsch.com/admodel.htm).

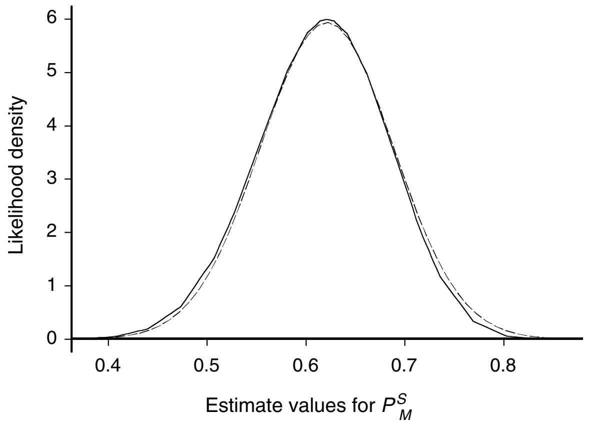

Figure 3

Profile likelihood (solid line) and asymptotic normal approximation (dashed line) for the likelihood confidence range about the estimate of P_M^S.

Results

The closed-form estimator for the proportion of lobsters that moved from the sanctuary (P_M^S) gave an estimate of 0.6206; i.e., about 62% of the lobsters tagged in Gleesons Sanctuary moved out in one year. The estimate obtained numerically, by maximizing the double-hypergeometric likelihood, yielded a value of 0.6212.

The small difference between the analytic and numerical estimates (0.09%) is presumably due to the use of the numerical approximation for the log-gamma function by the expansion of Equation 15. The close agreement suggests that the error introduced by that approximation is small.

The AD Model Builder parameter estimation software allows one to estimate confidence intervals of the movement-rate estimate in two ways: asymptotically, as diagonal elements of the covariance matrix, and by using a profile likelihood. Confidence intervals for the emigration rate estimate were thus obtained numerically from the hypergeometric likelihood by using both the asymptotic normal approximation and an exact profile likelihood. These gave 95% errors of 21.2% and 21.5% of the estimate, respectively. The approximate normal probability density function and the profile likelihood probability density function were also plotted (Fig. 3), yielding close agreement. Asymptotic confidence intervals therefore appear satisfactory for emigration proportion estimates not lying near the bounds of 0 and 1.

Intermediate calculation results (Table 2) included the recovery rate and movement rate (≥3 km) within the fished zone.

When independent estimates of exploitation rate are available, typically from stock assessment, the rate of tag reporting can be calculated from the tag-estimated recovery rate. The exploitation rate (yearly proportion of legal-size lobsters harvested) for the recapture year and location of the present study (the 1995 northern zone rock lobster season) was estimated to be 26% (Ward et al.[3]) by using total yearly effort and catches by weight and number and a vector of weights at age. The tag-recovery rate of 11.3% (Table 2) is the estimated proportion of tagged lobsters that were captured and for which tags were reported. Thus the estimated tag-reporting rate (of those recaptured) is 0.113/0.26=43%. If tag shedding and natural mortality were also incorporated as additional causes for nonrecovery, the estimate would fall in the neighborhood of a 50% tag-reporting rate. This estimated level of tag-reporting falls within the range considered probable by fishermen. Thus, the recovery-rate estimate falls within a plausible range of values, adding confidence that the tag-recovery data are consistent with external estimates of exploitation rate.

Substantial movement of *Jasus edwardsii* out of a marine sanctuary was previously observed in New Zealand (Kelly and MacDiarmid, 2003) but not in Tasmania (Gardner and Ziegler[4]). Long-distance movement of this genus was also observed in New Zealand (Booth, 1997) but was much less common in Tasmanian *Jasus edwardsii* populations (Gardner et al., in press).

Discussion

The emigration-rate derivation above combined recapture-and tag-conditioned movement proportions. Both ways to define a movement rate were used to constrain the range of solutions for both analytic and numerical estimators. Equating these two definitions for movement proportion reduced the degrees of freedom by 1, thereby circumventing the absence of a count of recaptured lobsters from within the fished zone.

Previous estimators of movement rates among spatial cells from tag-recovery data have used either tag- or recapture-conditioned approaches. Hilborn (1990; see also Quinn and Deriso, 1999) developed a tag-conditioned movement-rate estimator. This estimator generally requires prior knowledge of the tag reporting rate. Schwarz et al. (1993) employed data consisting of simultaneous tag releases and recaptures repeated over a number of years at the same time each year to estimate movement, survival, and recovery rates in each spatial stratum. Schwarz et al. (1993) presented a general formulation for modeling this multiple yearly tag-recovery data set, extending a series of estimators for movement and survival (Arnason, 1972, 1973), and estimated the rate of tag recovery. Brownie et al. (1993) generalized the estimator of Schwarz et al. to non-Markovian movement rates. McGarvey and Feenstra (2002), following Hilborn, used the less costly and more commonly available single tag-recovery data employed in the present study but adopted a recapture-conditioned approach for estimating yearly movement rates. With "numbers recaptured" appearing in both the numerator and denominator, all nonspatially dependent sources of variation (such as tag reporting and shedding, short- and long-term tag-induced mortality, and natural mortality) cancel from the predicted recapture-conditioned likelihood proportions. This procedure permits a corresponding reduction in the prior information required to obtain unbiased movement estimates.

When recapture times vary, movement estimation is sensitive to spatial differences in mortality rate, notably between tag and recapture cells. Assuming that the nonreporting rate is unknown, mortality can be inferred from single tag-release information only imprecisely, for example by using mean tagged time at large. For this reason externally obtained mortality estimates, typically from stock-assessment models using fishery data, can be usefully combined with single tag recoveries in movement estimation. Hestbeck (1995) showed, when survival differs by cell, that ignoring the time of movement between yearly samples could bias movement estimates. McGarvey and Feenstra (2002) made explicit the variation in residence time and thus survival in source (tag-release) and destination (recapture) cells for each recaptured animal. By using prior knowledge of a migration season, migration source cell and destination cell residence times can be approximated as the time from the date of tag release to an assumed fixed (yearly) date of movement, and from that date to the date of recapture. These residence times are used in exponential survival factors that differ spatially given externally estimated fishing mortality rates in each cell.

For the data set available from Gleesons Landing, all tagged animals were released during the peak fishing season (mid-summer). Thus recoveries from the following fishing season had a mean and mode near the desired one-year-at-large. In future tag-recovery studies, where a yearly movement rate is sought, a similar choice for timing of tag releases, namely during the season of highest fishery catches, should yield a peak in recaptures a year later. Schwarz et al. (1993) employed this strategy with their multiple yearly tag-recovery data sets.

In the estimator presented above, variations in expected recovery numbers versus time, notably due to survival, were neglected. The small sample (33 recoveries between 0.5 and 1.5 years from the sanctuary) and lack of recaptures from within the sanctuary necessitated more modest estimation goals. Among data classes available for movement analysis, notably 1) multiple yearly tag recaptures by researchers in all cells, 2) multiple yearly tag recoveries where recapture is by fishermen (or

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[3] Ward, T. M., R. McGarvey, Y. Xiao, and D. J. Brock. 2002. Northern zone rock lobster (*Jasus edwardsii*) fishery. South Australian Fisheries Assessment Series Report 2002/04b, 109 p. Aquatic Sciences, South Australian Research and Development Institute (SARDI); P.O. Box 120, Henley Beach, South Australia 5022, Australia.

[4] Gardner, C., and P. Ziegler. 2001. Are catches of the southern rock lobster *Jasus edwardsii* a true reflection of their abundance underwater? Tasmanian Aquaculture and Fisheries Institute Final Report. TAFI (Tasmanian Aquaculture and Fisheries Institute), University of Tasmania, Private Bag 49, Hobart TAS 7001, Australia.

hunters) in all cells, 3) single tag recoveries by fishermen in all cells, and 4) the data set employed in the present study of single-tag recoveries by fishermen in one of two cells, the latter represents the low end in quality and quantity of information about movement and survival.

A time-dependent approach could theoretically extend the approach of McGarvey and Feenstra (2002) to make explicit the residence times of each recaptured individual in the fishing zone and sanctuary, respectively, and thus make explicit differences in the predicted survival rate before and after movement. However without prior knowledge of when movement took place for each recaptured lobster, a modified likelihood method is called for, requiring integration over the probable movement times between tag release and recapture. This extension of residence-time-dependent movement estimators to variable times of movement remains a topic for future research.

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