SCRS/2013/031 Collect. Vol. Sci. Pap. ICCAT, 70(6): 2868-2888 (2014)

A SIMULATED CAPTURE-RECAPTURE MODEL FOR ESTIMATING MORTALITY AND STOCK MIXING RATES OF MIGRATORY ATLANTIC FISHES

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SUMMARY

A capture-recapture model for estimating the natural mortality, fishing mortality and migration rates of fishes migrating between two regions was outlined and simulation tested. Results were used to evaluate model sensitivity to target and nuisance parameters, and generate estimates of parameter bias and variance across a range of tagging efforts. Four populations were simulated using life-history parameters and fishing mortality estimates from recent assessments of bluefin tuna, yellowfin tuna, albacore, and blue marlin. Simulations revealed that unbiased estimates of natural and fishing mortality can be obtained from conventional tagging programs when coupled with electronic tagging studies that provide accurate estimates of instantaneous migration rates, a handling study to evaluate tagging mortality and tag retention, and tag return information from scientific observer programs, fishing fleet reported tags, or both. When recapture information is provided by fishing fleets exclusively, a high reward tagging study is needed to estimate fleet reporting rates and correct for under-reporting of tagged fish. The framework can be expanded to include age-structure, parameter heterogeneity or overdispersion, or to integrate multispecies or multiple fleet tagging information.

RÉSUMÉ

On a décrit et testé par simulation un modèle de capture-récupération pour estimer la mortalité naturelle, la mortalité par pêche et les taux de migration des poissons migrant entre deux régions. Les résultats ont servi à évaluer la sensibilité du modèle aux paramètres cibles et de nuisance et à créer des estimations des biais et des variances des paramètres sur une gamme d'efforts de marquage. Quatre populations ont été simulées à l'aide de paramètres du cycle vital et d'estimations de la mortalité par pêche provenant de récentes évaluations sur le thon rouge, l'albacore, le germon et le makaire bleu. Les simulations ont révélé que des estimations non-biaisées de la mortalité naturelle et par pêche peuvent être estimées des programmes de marquage conventionnel lorsque ceux-ci sont conjugués à des études de marquage électronique qui fournissent des estimations précises des taux de migration instantanée, une étude de manipulation visant à évaluer la mortalité par marquage et la rétention des marques, et des informations sur la récupération des marques des programmes d'observateurs scientifiques, les marques déclarées par la flottille de pêche, ou les deux. Lorsque les informations sur les récupérations sont exclusivement fournies par les flottilles de pêche, une étude de marquage dotée d'une forte récompense est nécessaire pour estimer les taux de déclaration des flottilles et corriger la sous-déclaration des poissons marqués. Le cadre peut être élargi afin d'englober la structure démographique, l'hétérogénéité ou la surdispersion des paramètres, ou bien afin d'intégrer l'information de marquage plurispécifique ou multi-flottilles.

RESUMEN

Se describe y se prueba mediante simulación un modelo de captura-recaptura para estimar la mortalidad natural, la mortalidad por pesca y las tasas de migración de los peces que migran entre dos regiones. Los resultados se utilizaron para evaluar la sensibilidad del modelo a parámetros objetivo y molestia y para generar estimaciones de la varianza y el sesgo de los parámetros en todo el rango de esfuerzos de marcado. Se simularon cuatro poblaciones utilizando parámetros del ciclo vital y estimaciones de la mortalidad por pesca de evaluaciones recientes de atún rojo, rabil, atún blanco y aguja azul. Las simulaciones

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revelaron que las estimaciones no sesgadas de la mortalidad natural y por pesca pueden obtenerse a través de programas de marcado convencional cuando se unen a estudios de marcado electrónico que proporcionan estimaciones precisas de tasas de migración instantánea, un estudio de manipulación para evaluar la mortalidad por marcado y la retención de marcas y la información sobre marcas recuperadas procedente de programas de observadores científicos, marcas declaradas por la flota pesquera o ambos. Cuando la información sobre recaptura la proporcionan exclusivamente las flotas pesqueras, es necesario un estudio de marcado con recompensas altas es necesario para estimar las tasas de comunicación de la flota y corregir la infracomunicación de los peces marcados. El marco puede ampliarse para incluir información sobre estructura de la edad, heterogeneidad de parámetros o sobredispersión, o para intergrar información de marcado multiespecífica o de múltiples flotas.

KEYWORDS

Tagging, Simulation, Migrations, Natural mortality, Catchability

1. Introduction

Considerable uncertainty exists around the population dynamics and fishing mortality rates of migratory pelagic fishes in the Atlantic Ocean (Patterson et al. 2001, Restrepo et al. 2003, Fromentin and Ravier 2005). Accurate estimates of key life-history parameters, including natural mortality, growth and stock mixing rates are needed for the purposes of improving the accuracy of stock assessments and providing sound scientific advice to international stakeholders (Fromentin 2003, Drew et al. 2006). Estimates of annual fishing mortalities from fishery-independent data sources are needed to validate stock assessment results and reduce scientific uncertainty (NRC 1998, Rose and Cohan 2003). The potential benefits of a carefully designed and implemented capture-recapture study include unbiased estimation of species population dynamics parameters and fishing mortality rates and measures of the uncertainty of these parameters.

Absolute abundance, mortality, growth, and migration rates can often be efficiently estimated using capture-recapture models, and a wealth of information is available on the statistical framework for estimating population dynamics from tagging studies (Pollock et al. 2002, Seber 2002, Williams et al. 2002). In open systems such as the Atlantic Ocean, relatively complex capture-recapture models are required to account for sources of mortality, migration, tag loss, and under-reporting of harvested animals. These parameters are generally confounded, and unbiased parameter estimation from a single tagging study is often not possible. It is therefore necessary to couple information from multiple tagging efforts, each aimed at estimating specific target and nuisance parameters (Pine et al. 2003). Kurota et al. (2009), for example, outlined a sequential tagging model that utilized information from electronic tagging to estimate fishing mortality rates over time from conventional tagging data. They demonstrated the utility of coupling information from multiple tagging efforts, and a similar approach was adopted for this analysis.

I programmed and simulated a statistical capture-recapture model aimed at estimating the natural mortality, fishing mortality, and stock mixing rates of four Atlantic migratory fishes, including bluefin tuna (*Thunnus thynnus*), yellowfin tuna (*Thunnus albacares*), albacore (*Thunnus alalunga*), and blue marlin (*Makaira nigricans*).

Key model components included estimation of handling mortality and conventional tag shedding from handling studies, estimation of instantaneous migration rates from pop-up satellite archival tag data, estimation of reporting rates from high reward tag returns, and estimation of natural and fishing mortality from conventional tag returns by scientific observers or fleet reported tags. Study design, data requirements, and model sensitivity to key parameters are evaluated and discussed.

2. Material and Methods

An open capture-recapture model was simulated to evaluate target and nuisance parameter estimate bias and variation across a range of tagging efforts and assuming different life-history parameters (**Tables 1** and **2**). The model structure was similar to the multi-year cohort tag return model of Polacheck et al. (2006), and using a sequential Bayesian approach similar to Kurota et al. (2009) in which electronic and conventional tag information were assessed sequentially. The model structure differed from that of Polacheck et al. (2006) in that inferences are made from the tagged population, absolute abundance is not estimated directly, instantaneous migration rates between two geographic regions are incorporated, and tagging mortality and tag loss are not assumed to be negligible. Model structure differed from Kurota et al. (2009) in that a single stage-class cohort was assessed; however, the model framework can be expanded to include individual age-classes for estimation of age-specific mortality and migration rates. Posterior migration probabilities from pop-up satellite archival tagging data were used as prior probabilities in a conventional tagging capture-recapture simulation. Natural mortality was treated as a target parameter and was estimated along with catchability. Tagging mortality and tag shedding were treated as nuisance parameters with posterior probabilities estimated from handling studies utilizing conventional or electronic tags. Prior distributions for migration, tagging mortality, and tag shedding rates were assumed to have a binomial error structure based on the number of released animals per tag type and the observed success rates. Conventional tag returns were assumed to be from scientific observer programs with known coverage, or reported by fishing fleets with reporting rate estimated from high reward conventional tags. Additional model assumptions are outlined below:

- The study duration was four years
- The study population occurred within two distinct geographic regions
- A proportion of the population in each region migrated to the other region; migration occurred instantaneously throughout the study period
- Natural mortality occurred instantaneously throughout the study period
- Tagging was conducted by biologists within both study regions during years one through three
- Every tagged individual received a unique ID number
- Tagging events occurred annually during discrete sample periods prior to fishing seasons
- A proportion of tagged fish died as a result of handling and tagging; handling mortality rates were discrete
- A proportion of tagged fish that survived the handling procedure shed their tag; tag shedding rates were discrete
- Fishing occurred in each study region after the annual tagging events
- Fishing effort varied across study regions and years
- The probability of capture (p) was modeled as a function of fishing effort (E) and a gear catchability coefficient (q) defined by the following equation:

$$p=1-e^{-qE} = 1-e^{-F}$$

- Fishing effort within a region and year was uniformly distributed between a defined minimum and maximum so that the observed fishing mortality ($F=qE$) was a uniform random number with set boundaries representative of estimates from recent stock assessments
- A proportion of the catch in each region was scientifically observed for tagged individuals
- All tagged individuals in the scientifically observed catches were recorded
- Tagged individuals captured by fishing fleets were reported imperfectly
- The tag ID, date and study region were recorded upon recapture or were reported by fishing fleets
- All recaptured fish were removed by the fishery, and therefore only one recapture event was possible for each tagged individual

Given the model assumptions, there are a discrete number of possible outcomes (capture histories) for each individual tagged and released within a study region and year. Appendix 1 lists the possible capture histories of fish tagged during years one through three in each region, the definitions of these capture histories, and the associated probabilities. **Table 1** contains a list of the parameters contained within the probability statements and their definitions. Target parameters included the instantaneous natural mortality rate, the capture probability modeled as an exponential function of fishing mortality equal to the product of the fleet catchability coefficient and fishing effort within a region, and the stock mixing rates between region 1 and 2 and vice versa. Nuisance parameters included the discrete handling mortality rate, tag shedding rate, and fleet reporting rates in regions 1 and 2. The fleet reporting rates were equivalent to the proportion of the total catch in each region that is scientifically observed, and these parameters were interchangeable in the model. In either case, the reporting rate parameters represent the proportion of recaptured individuals in each region with tag return information.

Predicted numbers of returned tags per region and year (i.e. number of observations per capture history) were simulated as random deviates from the multinomial probability distribution given the number of conventionally tagged fish released and the probability of each capture history defined in Appendix 1. The log-likelihood (LL) function associated with tag return data from each tagging event was the $\log_e$-transformed multinomial probability mass function given the number of tagged fish released and the probability of each capture history:

$$LL_{R,Y}(x_{1\to k}|N, Pr_{1\to k}) = log_e(N!) - \sum_{i=1}^{k} log_e(x_i!) + \sum_{i=1}^{k}[x_i \cdot log_e(Pr_i)]$$

where,
LL is the log-likelihood value
R is the study region
Y is the study year
N is the number of marked fish released within the study region during a year
x_i is the observed number of tagged fish for each capture history i
Pr_i is the probability of each capture history i
k is the total number of capture histories associated with each tagging event

The total log-likelihood function was the sum of the log-likelihoods of each tagging event across study regions and years:

$$Total\ LL = LL_{1,1} + LL_{2,1} + LL_{1,2} + LL_{2,2} + LL_{1,3} + LL_{2,3}$$

Using this model framework, it was possible to simulate data from a four-year capture-recapture study conducted on a variety of migratory Atlantic fishes representing a range of life histories and supported fisheries, including bluefin tuna, yellowfin tuna, albacore, and blue marlin (**Table 2**). Parameter estimate bias and coefficient of variation across a range of tagging study efforts were evaluated using results from 10,000 iterations per model simulation. Tagging efforts included a low effort scenario (1000 conventional tags per study region per year, 100 high reward tags per study region released in year one, 100 fish held for observation, and 50 pop-up satellite archival tags per region released in year one), medium effort scenario (2000 conventional tags per study region per year, 200 high reward tags per study region released in year one, 200 fish held for observation, and 100 pop-up satellite archival tags per region released in year one), and high effort scenario (5000 conventional tags per study region per year, 500 high reward tags per study region released in year one, 500 fish held for observation, and 200 pop-up satellite archival tags per region released in year one). The statistical code for the model, written in program R, is provided in Appendix 2.

3. Results and Discussion

Model simulations indicated that unbiased estimates of natural mortality and catchability can be acquired from conventional tag return data when accurate estimates of migration rates, tagging mortality, tag shedding, and reporting rates are obtained from coupled tagging studies using pop-up satellite archival, conventional and high reward tags (**Figure 1**). At low tagging effort, natural mortality estimate mean bias ranged from approximately 10% for blue marlin to less than 1% for yellowfin tuna and albacore (**Table 3**). Natural mortality coefficient of variation ranged from 0.82 for blue marlin to 0.15 for yellowfin tuna under the low tagging effort scenario. At high tagging effort, mean natural mortality estimate bias was less than 1% for all four populations. Natural mortality estimate coefficient of variation ranged from 0.44 for blue marlin to 0.07 for yellowfin tuna under the high tagging effort scenario. Catchability estimate mean bias was less than 3% for all populations under all three effort scenarios (**Table 3**). Catchability estimate coefficient of variation was highest for blue marlin and bluefin tuna under the low effort scenario at 0.28, and was less than 0.2 for all other simulated populations and effort scenarios. In general, mortality estimates were less biased and most accurate for species with higher natural and fishing mortality (yellowfin tuna and albacore), and parameter estimates for species with low natural mortality ranged considerably (95% CI of estimate bias = -68 to 60% for bluefin tuna, -80 to 90% bias for blue marlin under the high effort scenario). Catchability was estimated with relatively high accuracy (less than 1% mean bias across populations), and low uncertainty (95% CI of estimates bias was plus or minus 26% or less) for all populations in the high tagging effort model.

The conventional tag capture-recapture model is dependent on accurate information from coupled tagging studies. If estimates of tagging mortality, tag shedding, migration, and reporting rates are biased, then estimates of natural and fishing mortality will be biased. The model framework incorporated parameter estimate uncertainty from multiple studies, with estimated variances assumed to be binomial or multinomial, depending on tag type and study (**Figures 2-5** display the posterior probability distributions used as priors in the mortality estimation model). Migration rates can be estimated from individual movement data of satellite archival tagged fish (e.g., Miller and Andersen 2008). Satellite archival tag duration of 6 months was assumed in the simulation; however, longer tag duration may produce more accurate movement probability estimates with optimal tag duration equal to the study duration. Tagging mortality and tag shedding can be estimated by containment studies utilizing conventional tags or via electronic tag data (Brill et al. 2002, Hightower et al. 2001, Pollock and Pine 2007) and from double-tagging studies (Fabrizio et al. 1999). The former method of estimating release mortality may be preferred since fish can be captured and handled in the same manner as those being released, and electronically tagged individuals may experience different handling procedures, stressors, or modified behavior (e.g., Close et al. 2003). When conventionally tagged fish are recorded by scientific observers, the reporting rate parameters are equal to the proportion of the catch observed in each region. If those proportions are known, then fishing fleet reporting rates can be estimated from observer and fleet reported tag returns without a high reward program. When tag return information is reported by fishing fleets, exclusively, then it is necessary to estimate fleet reporting rates from a high reward tagging study or alternative method.

The model presented here represents a simplistic base model from which more complicated models can be constructed and evaluated based on the known life-histories and fisheries of individual age classes, life history stages or species. The estimated bias and variances for a modeled sample size will vary depending on migration patterns, fishing effort, and other parameters associated with the target species or age class. Regardless, the statistical framework can be applied to a broad range of species, age classes, fishing fleets, and tagging efforts. Under the simple structure presented here, the data requirements are relatively minimal. The first data needed are individual PSAT track data for estimation of instantaneous migration rates between regions and to validate mixing assumptions. The second data required are estimates of tagging mortality and tag loss from a containment study, electronic tag data, or both (Pollock and Pine 2007). The final data requirements include the numbers of conventionally tagged fish released in each region in years 1 through 3, the fleet fishing efforts and catch per region and year, the ID numbers of recaptured fish in scientific samples in each region and year, and the proportions of the catches that are observed for tags in each region and year.

The assumption of permanent migration was inherent in the model. Since conventionally tagged fish were recaptured a maximum of once, it was not possible to document multiple migration events between regions. A fish captured in the region it was tagged was assumed to have remained in the region the entire time, and a fish that migrated was assumed to remain in the new region for the remainder of the study period. If during study implementation, the satellite archival tag information indicated that significant mixing occurs between regions, the model could be restructured to account for return migrations or continuous mixing of individuals. Another key model assumption was discrete tagging and fishing seasons. In the simulation, an average time (t) between tagging and fishing seasons equal to three months was assumed. If tagging and fishing occurred continuously throughout the year, the model should be restructured so that probabilities are based on individual times at large (e.g., Lebreton et al 2009) instead of an average time between capture and recapture events. Additionally, tag return information was modeled for a single fleet, but multiple fleet catch and tag return information could be incorporated to better inform natural and fishing mortality estimates.

The high effort study design is ambitious, with the goal of having over 5,000 fish tagged annually in each study region. Study implementation would likely require a large cooperation amongst biologists and fisherman throughout the range of the populations, and distributing the tagging effort across the entire geographic range is ideal for meeting the assumption that tagged individuals are representative of the study population (Brownie et al. 1985). One example scenario is to distribute the effort across 20 cooperating parties, each with the goal of releasing 250 conventionally tagged individuals within a defined geographic region, as well as 10 satellite tagged individuals, 25 high reward tagged fish, and retaining a number of conventionally tagged individuals for a containment study to estimate handling mortality and tag loss. The logistics of implementing such a large-scale tagging effort requires further discussion and expertise from regional scientists and fisherman.

A multispecies tagging study design provides the benefit of greater efficiency compared to disparate species tagging efforts, and produces measures of community metrics including species composition (Lauretta et al. 2013), richness (Boulinier et al. 1998), and diversity (Nichols 1983). Sampling efforts in each region might focus on tagging multiple species of migratory pelagic fishes so that natural and fishing mortality estimates are acquired for a range of populations. Estimates are likely to be more accurate and precise for species that are regional abundant and can be tagged in greater numbers; therefore, distribution of tagging effort across a large geographic range is ideal for a multispecies tagging program. Lastly, estimation of mortality rates and abundances for pelagic communities can provide insight into the trophic dynamics that structure predator and prey populations, and provide information on how communities, as a whole, respond to harvest and environmental change.

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Table 1. Capture-recapture model parameters and definitions.

Parameter	Definition
M	Instantaneous natural mortality rate
m_{12}	Instantaneous migration rate from region 1 to 2
m_{21}	Instantaneous migration rate from region 2 to 1
T	Discrete handling/tagging mortality rate
s	Discrete tag shedding rate
q	Fleet catchability coefficient
r_1	Observer coverage/Fleet reporting rate region 1
r_2	Observer coverage/Fleet reporting rate region 2
t	time between tagging and fishing events

Table 2. Parameter estimates used in the model simulations of four migratory Atlantic fishes.

	Bluefin tuna	Yellowfin tuna	Albacore	Blue marlin
Natural mortality (M)	0.14	0.70	0.40	0.10
Catchability coefficient (q)	0.0001	0.0001	0.0001	0.0001
Effort (E)	500-1000	3000-4000	4000-5000	500-1000
Fishing mortality (F = qE)	0.05-0.1	0.3-0.4	0.4-0.5	0.05-0.1
Migration rate region 1 to 2 (m_{12})	0.05	0.05	0.01	0.20
Migration rate region 2 to 1 (m_{21})	0.10	0.05	0.01	0.20
Tagging/handling mortality (T)	0.10	0.15	0.20	0.10
Tag shedding (s)	0.05	0.04	0.03	0.05
Observer coverage/reporting rate in region 1 (r_1)	0.10	0.10	0.10	0.10
Observer coverage/reporting rate in region 2 (r_2)	0.10	0.10	0.10	0.10

Table 3. Natural mortality and catchability estimate bias and coefficients of variation.

	Bluefin tuna			Yellowfin tuna			Albacore			Blue marlin		
Effort scenario	Low	Med	High	Low	Med	High	Low	Med	High	Low	Med	High
Conventional Tags/Year*Region	1000	2000	5000	1000	2000	5000	1000	2000	5000	1000	2000	5000
Handling Study Tags	100	200	500	100	200	500	100	200	500	100	200	500
High Reward Tags/Region	100	200	500	100	200	500	100	200	500	100	200	500
Electronic Tags/Region	50	100	200	50	100	200	50	100	200	50	100	200
Mean % bias M estimates	5.4	2.4	0.8	0.7	0.4	0.2	-0.2	0.2	-0.1	10.3	2.9	0.7
95LL % bias M estimates	-100	-99	-64	-28	-20	-13	-42	-29	-19	-100	-100	-86
95UL % bias M estimates	155	109	68	32	22	14	41	30	18	210	147	90
CV of M estimates	0.67	0.51	0.33	0.15	0.11	0.07	0.21	0.15	0.09	0.82	0.66	0.44
Mean % bias q estimates	-1.7	-2.8	-3.1	1.6	0.5	0.1	1.0	0.5	0.1	2.2	0.5	0.3
95LL % bias q estimates	-44	-35	-24	-33	-24	-16	-27	-21	-13	-41	-31	-21
95UL % bias q estimates	64	39	22	47	30	18	39	26	16	67	42	26
CV of q estimates	0.28	0.20	0.12	0.20	0.14	0.09	0.17	0.12	0.08	0.28	0.19	0.12

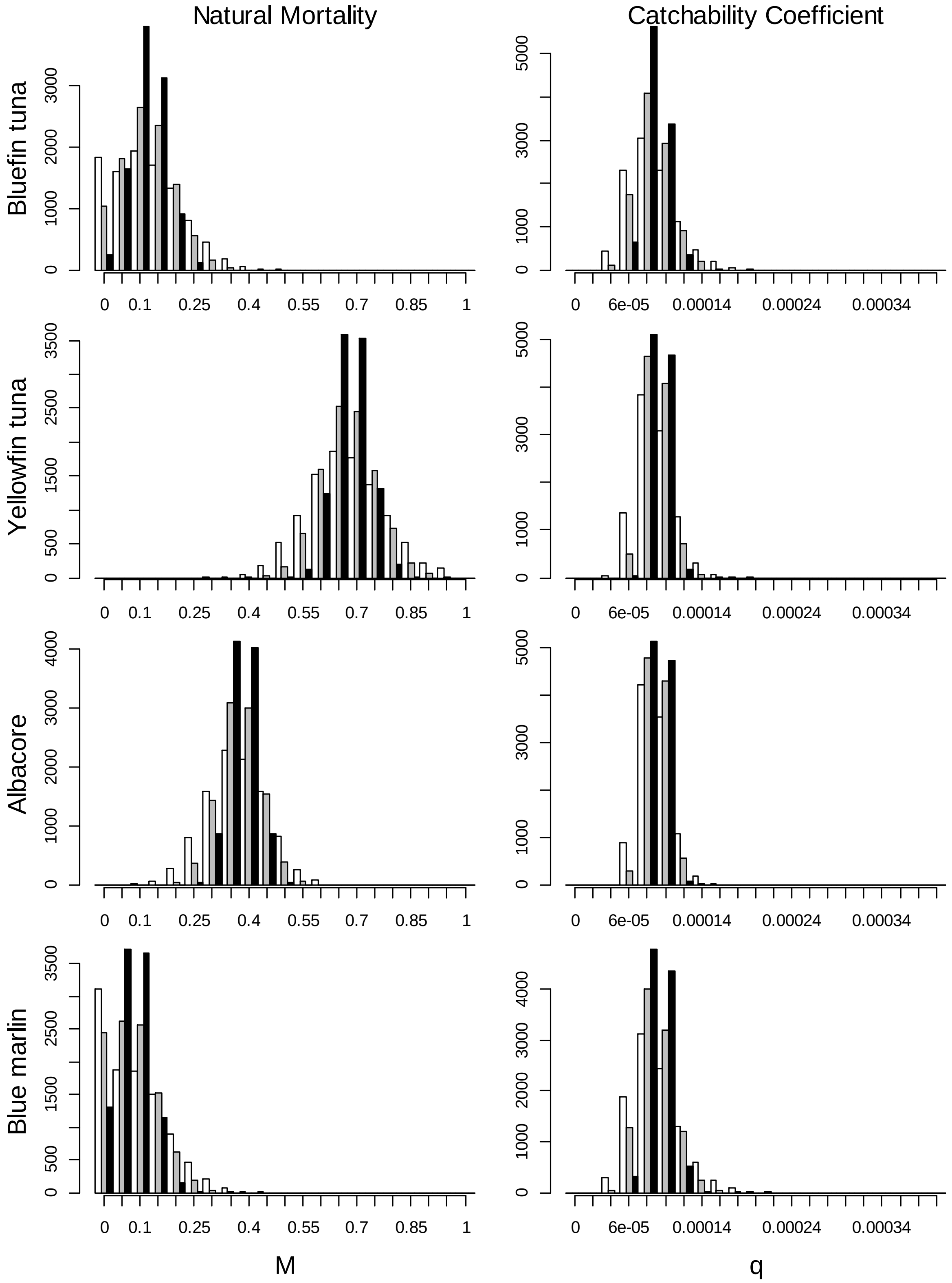

Figure 1. Distributions of natural mortality and catchability estimates from 10,000 simulations of the capture-recapture model under the low effort (white bars), medium effort (gray bars), and high effort (black bars) tagging scenarios.

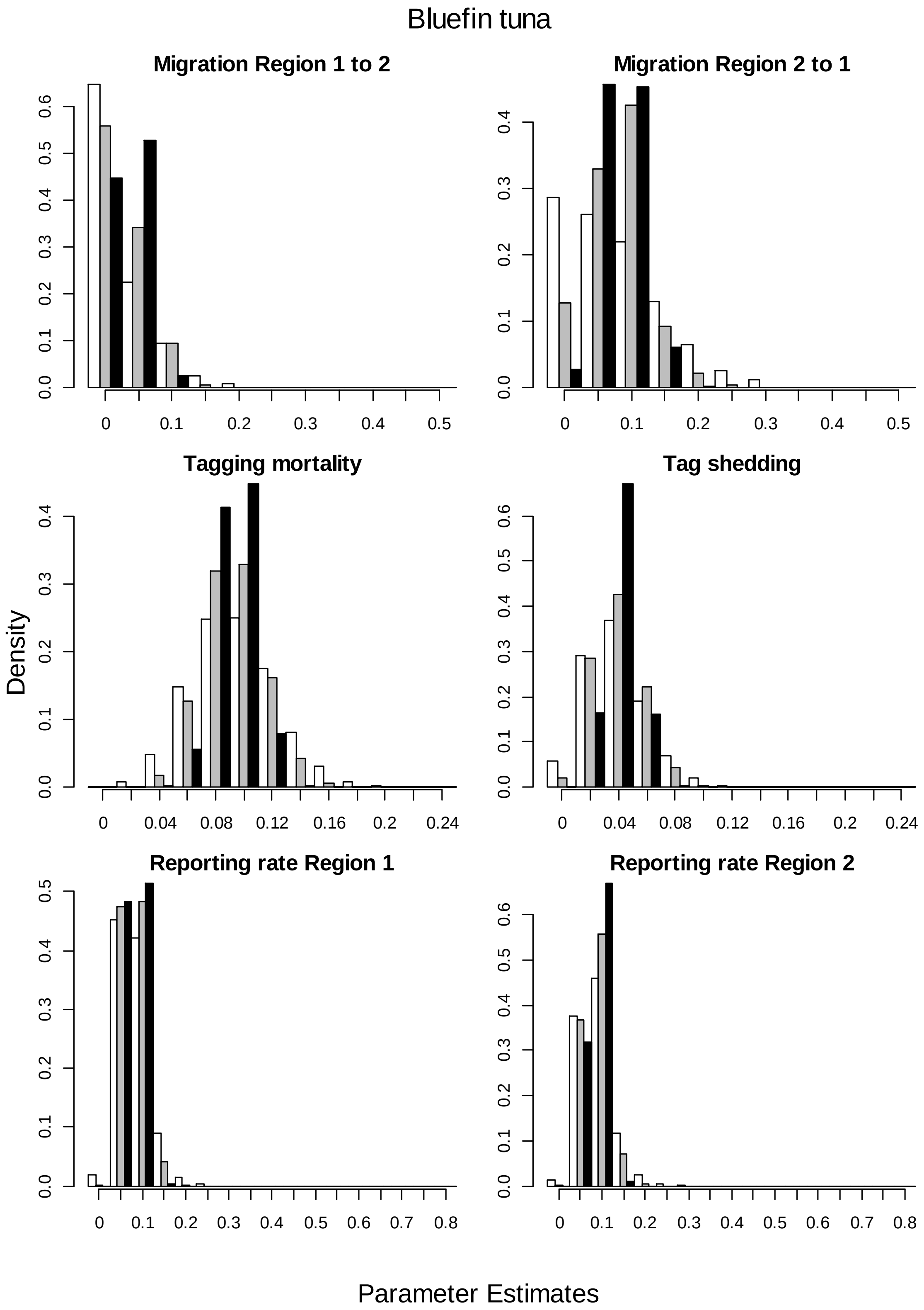

Figure 2. Simulated posterior distributions of migration rates, tag mortality, tag shedding, and reporting rates estimated from coupled tagging studies of bluefin tuna.

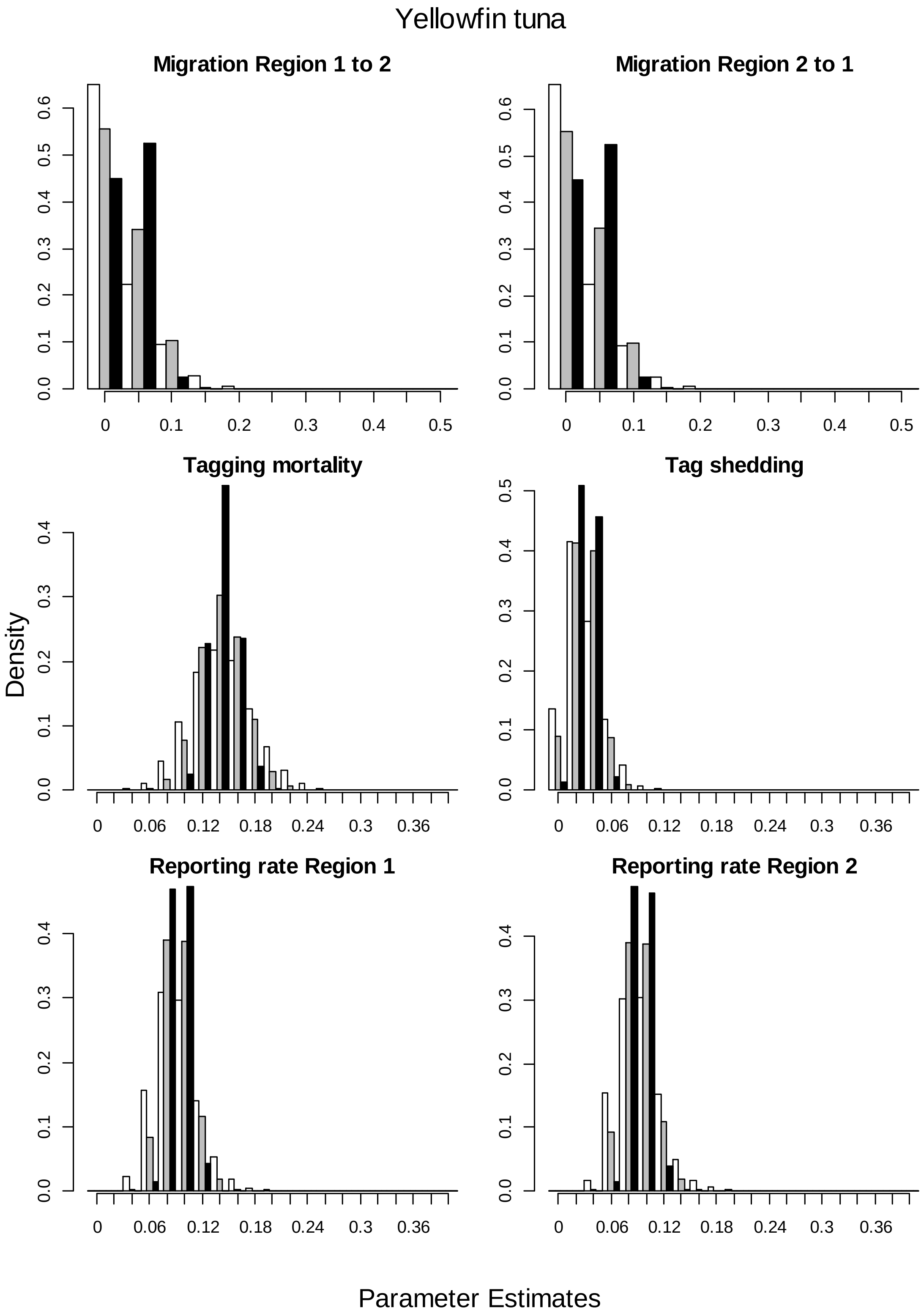

Figure 3. Simulated posterior distributions of migration rates, tag mortality and shedding, and reporting rates estimated from coupled tagging studies of yellowfin tuna.

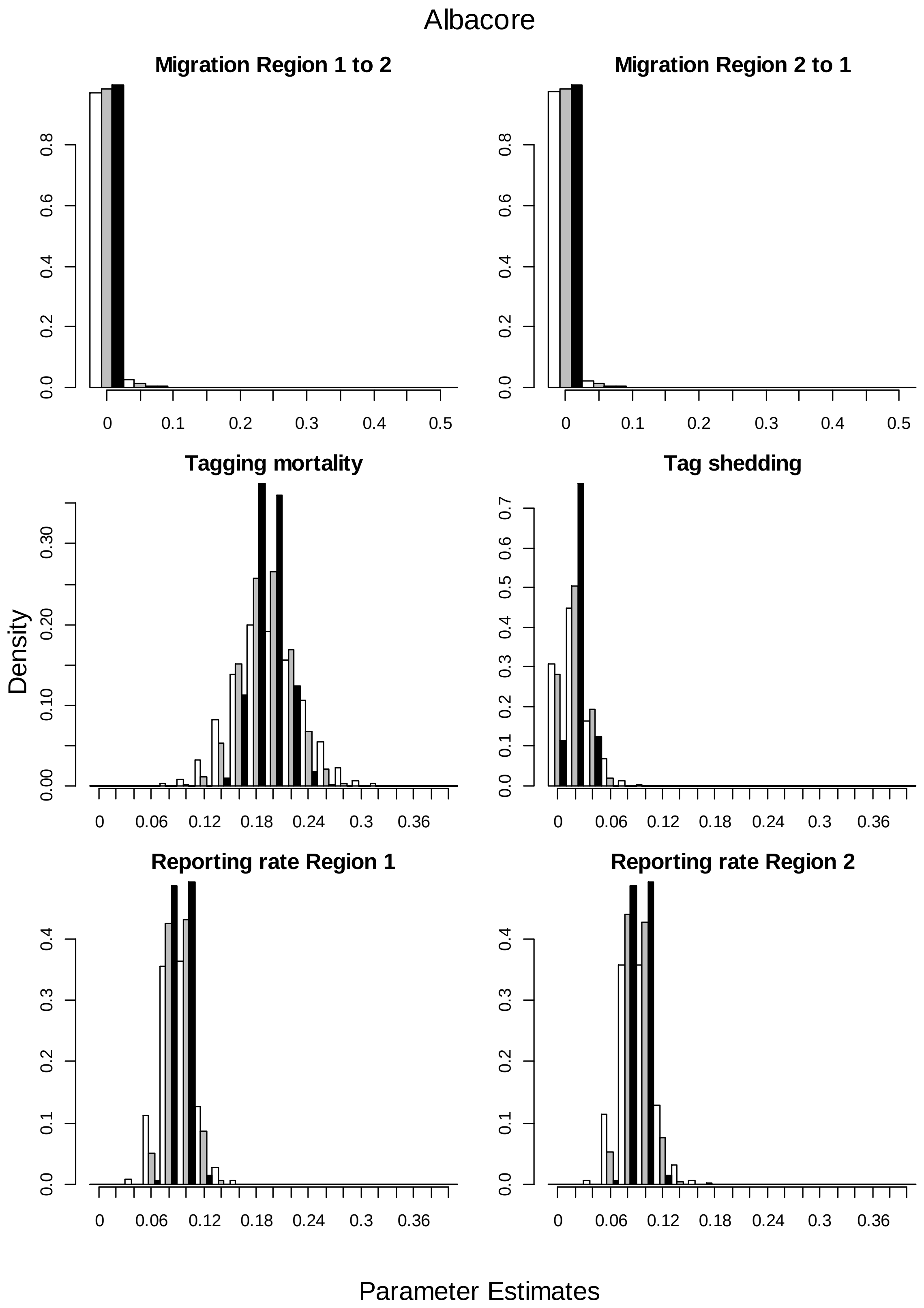

Figure 4. Simulated posterior distributions of migration rates, tag mortality and shedding, and reporting rates estimated from coupled tagging studies of albacore.

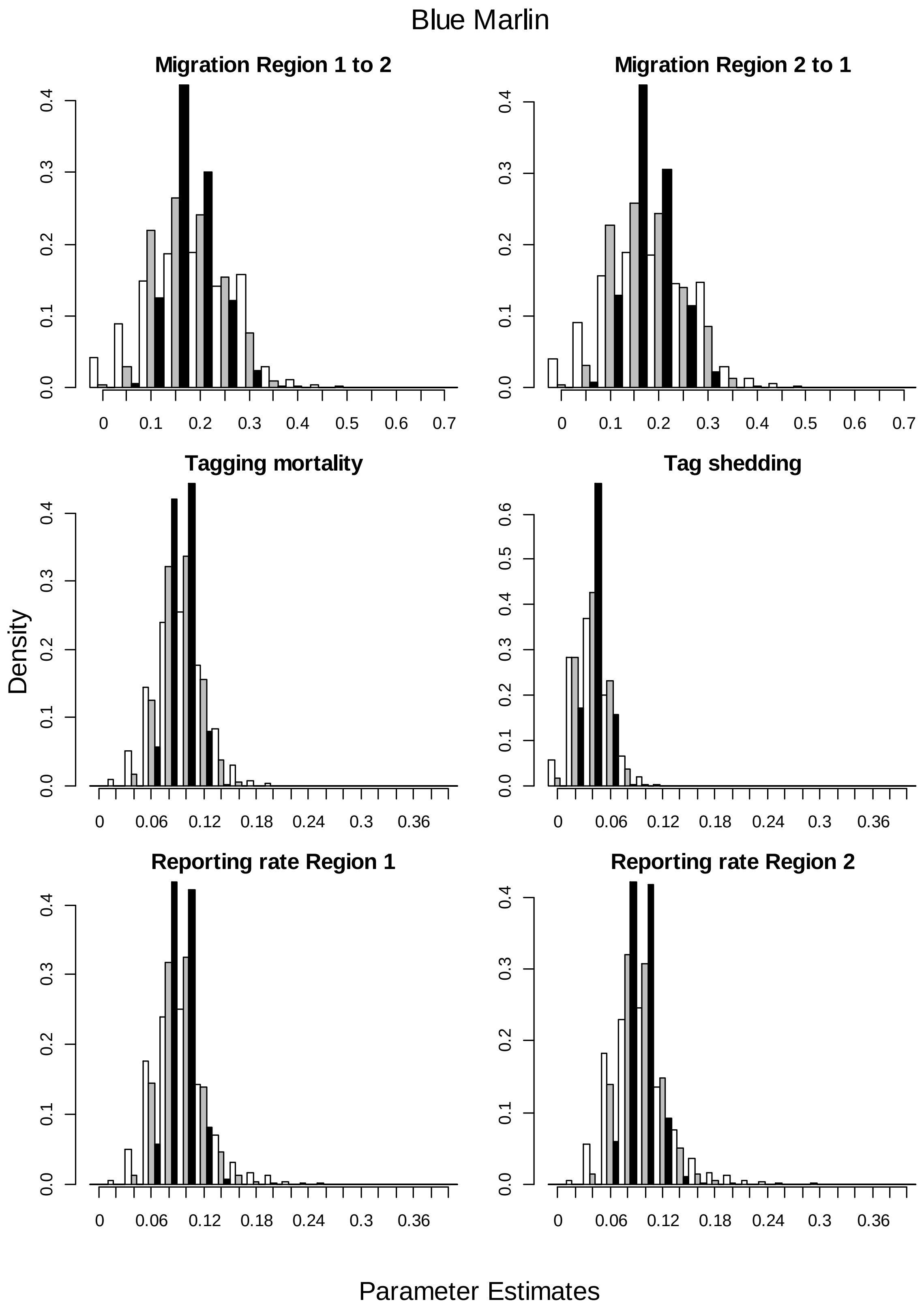

Figure 5. Simulated posterior distributions of migration rates, tag mortality and shedding, and reporting rates estimated from coupled tagging studies of blue marlin.

APPENDIX 1. Definitions of capture-recapture study outcomes (capture histories) and associated probability statements

OUTCOME	DEFINITION
11_1	fish tagged in region 1 during year 1 with tag returned in region 1 during fishing season 1
11_01	fish tagged in region 1 during year 1 with tag returned in region 1 during fishing season 2
11_001	fish tagged in region 1 during year 1 with tag returned in region 1 during fishing season 3
11_0001	fish tagged in region 1 during year 1 with tag returned in region 1 during fishing season 4
11_2	fish tagged in region 1 during year 1 with tag returned in region 2 during fishing season 1
11_02	fish tagged in region 1 during year 1 with tag returned in region 2 during fishing season 2
11_002	fish tagged in region 1 during year 1 with tag returned in region 2 during fishing season 3
11_0002	fish tagged in region 1 during year 1 with tag returned in region 2 during fishing season 4
11_0000	fish tagged in region 1 during year 1 with no tag return information
21_1	fish tagged in region 2 during year 1 with tag returned in region 1 during fishing season 1
21_01	fish tagged in region 2 during year 1 with tag returned in region 1 during fishing season 2
21_001	fish tagged in region 2 during year 1 with tag returned in region 1 during fishing season 3
21_0001	fish tagged in region 2 during year 1 with tag returned in region 1 during fishing season 4
21_2	fish tagged in region 2 during year 1 with tag returned in region 2 during fishing season 1
21_02	fish tagged in region 2 during year 1 with tag returned in region 2 during fishing season 2
21_002	fish tagged in region 2 during year 1 with tag returned in region 2 during fishing season 3
21_0002	fish tagged in region 2 during year 1 with tag returned in region 2 during fishing season 4
21_0000	fish tagged in region 2 during year 1 with no tag return information
12_01	fish tagged in region 1 during year 2 with tag returned in region 1 during fishing season 2
12_001	fish tagged in region 1 during year 2 with tag returned in region 1 during fishing season 3
12_0001	fish tagged in region 1 during year 2 with tag returned in region 1 during fishing season 4
12_02	fish tagged in region 1 during year 2 with tag returned in region 2 during fishing season 2
12_002	fish tagged in region 1 during year 2 with tag returned in region 2 during fishing season 3
12_0002	fish tagged in region 1 during year 2 with tag returned in region 2 during fishing season 4
12_0000	fish tagged in region 1 during year 2 with no tag return information
22_01	fish tagged in region 2 during year 2 with tag returned in region 1 during fishing season 2
22_001	fish tagged in region 2 during year 2 with tag returned in region 1 during fishing season 3
22_0001	fish tagged in region 2 during year 2 with tag returned in region 1 during fishing season 4
22_02	fish tagged in region 2 during year 2 with tag returned in region 2 during fishing season 2
22_002	fish tagged in region 2 during year 2 with tag returned in region 2 during fishing season 3
22_0002	fish tagged in region 2 during year 2 with tag returned in region 2 during fishing season 4
22_0000	fish tagged in region 2 during year 2 with no tag return information
13_001	fish tagged in region 1 during year 3 with tag returned in region 1 during fishing season 3
13_0001	fish tagged in region 1 during year 3 with tag returned in region 1 during fishing season 4
13_002	fish tagged in region 1 during year 3 with tag returned in region 2 during fishing season 3
13_0002	fish tagged in region 1 during year 3 with tag returned in region 2 during fishing season 4
13_0000	fish tagged in region 1 during year 3 with no tag return information
23_001	fish tagged in region 2 during year 3 with tag returned in region 1 during fishing season 3
23_0001	fish tagged in region 2 during year 3 with tag returned in region 1 during fishing season 4
23_002	fish tagged in region 2 during year 3 with tag returned in region 2 during fishing season 3
23_0002	fish tagged in region 2 during year 3 with tag returned in region 2 during fishing season 4
23_0000	fish tagged in region 2 during year 3 with no tag return information

OUTCOME PROBABILITIES

Pr(11_1)=$(1-T)(1-s)(e^{-(M+m_{12})t})(1-e^{-qE_{11}})r_1$
Pr(11_01) =$(1-T)(1-s)(e^{-(M+m_{12})(t+1)-qE_{11}})(1-e^{-qE_{12}})r_1$
Pr(11_001)=$(1-T)(1-s)(e^{-(M+m_{12})(t+2)-q(E_{11}+E_{12})})(1-e^{-qE_{13}})r_1$
Pr(11_0001)=$(1-T)(1-s)(e^{-(M+m_{12})(t+3)-q(E_{11}+E_{12}+E_{13})})(1-e^{-qE_{14}})r_1$
Pr(11_2)=$(1-T)(1-s)(e^{-Mt})(1-e^{-m_{12}t})(1-e^{-qE_{21}})r_2$
Pr(11_02)=$(1-T)(1-s)(e^{-M(t+1)})(1-e^{-qE_{22}})r_2[(1-e^{-m_{12}t})(e^{-qE_{21}})+(e^{-m_{12}t-qE_{11}})(1-e^{-m_{12}})]$
Pr(11_002) =
$(1-T)(1-s)(e^{-M(t+2)})(1-e^{-qE_{23}})r_2[(1-e^{-m_{12}t})(e^{-q(E_{21}+E_{22})})+(e^{-m_{12}t-qE_{11}})(1-$
$e^{-m_{12}})(e^{-qE_{22}})+(e^{-m_{12}(t+1)-q(E_{11}+E_{12})})(1-e^{-m_{12}})]$

Pr(11_0002)=
$(1-T)(1-s)(e^{-M(t+3)})(1-e^{-qE_{24}})r_2[(1-e^{-m_{12}t})(e^{-q(E_{21}+E_{22}+E_{23})})+(e^{-m_{12}t-qE_{11}})(1-$
$e^{-m_{12}})(e^{-q(E_{22}+E_{23})})+(e^{-m_{12}(t+1)-q(E_{11}+E_{12})})(1-e^{-m_{12}})(e^{-E_{23}})+$
$(e^{-m_{12}(t+2)-q(E_{11}+E_{12}+E_{13})})(1-e^{-m_{12}})]$

Pr(11_0000)=1
$-\sum(\mathrm{Pr\_11\_1}, \mathrm{Pr\_11\_01}, \mathrm{Pr\_11\_001}, \mathrm{Pr\_11\_0001}, \mathrm{Pr\_11\_2}, \mathrm{Pr\_11\_02}, \mathrm{Pr\_11\_002}, \mathrm{Pr\_11\_0002})$
Pr(21_2) = $(1-T)(1-s)(e^{-(M+m_{21})t})(1-e^{-qE_{21}})r_2$
Pr(21_02)=$(1-T)(1-s)(e^{-(M+m_{21})(t+1)-qE_{21}})(1-e^{-qE_{22}})r_2$
Pr(21_002)=$(1-T)(1-s)(e^{-(M+m_{21})(t+2)-q(E_{21}+E_{22})})(1-e^{-qE_{23}})r_2$
Pr(21_0002)=$(1-T)(1-s)(e^{-(M+m_{21})(t+3)-q(E_{21}+E_{22}+E_{23})})(1-e^{-qE_{24}})r_2$
Pr(21_1)=$(1-T)(1-s)(e^{-Mt})(1-e^{-m_{21}t})(1-e^{-qE_{11}})r_1$
Pr(21_01)=$(1-T)(1-s)(e^{-M(t+1)})(1-e^{-qE_{12}})r_1[(1-e^{-m_{21}t})(e^{-qE_{11}})+(e^{-m_{21}t-qE_{21}})(1-e^{-m_{21}})]$
Pr(21_001)=
$(1-T)(1-s)(e^{-M(t+2)})(1-e^{-qE_{13}})r_1[(1-e^{-m_{21}t})(e^{-q(E_{11}+E_{12})})+(e^{-m_{21}t-qE_{21}})(1-$
$e^{-m_{21}})(e^{-qE_{12}})+(e^{-m_{21}(t+1)-q(E_{21}+E_{22})})(1-e^{-m_{21}})]$

Pr(21_0001)=
$(1-T)(1-s)(e^{-M(t+3)})(1-e^{-qE_{14}})r_1[(1-e^{-m_{21}t})(e^{-q(E_{11}+E_{12}+E_{13})})+(e^{-m_{21}t-qE_{21}})(1-$
$e^{-m_{21}})(e^{-q(E_{12}+E_{13})})+(e^{-m_{21}(t+1)-q(E_{21}+E_{22})})(1-e^{-m_{21}})(e^{-E_{13}})+$
$(e^{-m_{21}(t+2)-q(E_{21}+E_{22}+E_{23})})(1-e^{-m_{21}})]$

Pr(11_0000)=1
$-\sum(\mathrm{Pr\_21\_1}, \mathrm{Pr\_21\_01}, \mathrm{Pr\_21\_001}, \mathrm{Pr\_21\_0001}, \mathrm{Pr\_21\_2}, \mathrm{Pr\_21\_02}, \mathrm{Pr\_21\_002}, \mathrm{Pr\_21\_0002})$
Pr(12_01)=$(1-T)(1-s)(e^{-(M+m_{12})t})(1-e^{-qE_{12}})r_1$
Pr(12_001)=$(1-T)(1-s)(e^{-(M+m_{12})(t+1)-qE_{12}})(1-e^{-qE_{13}})r_1$
Pr(12_0001)=$(1-T)(1-s)(e^{-(M+m_{12})(t+2)-q(E_{12}+E_{13})})(1-e^{-qE_{14}})r_1$
Pr(12_02)=$(1-T)(1-s)(e^{-Mt})(1-e^{-m_{12}t})(1-e^{-qE_{22}})r_2$
Pr(12_002)=$(1-T)(1-s)(e^{-M(t+1)})(1-e^{-qE_{23}})r_2[(1-e^{-m_{12}t})(e^{-qE_{22}})+(e^{-m_{12}t-qE_{12}})(1-e^{-m_{12}})]$
Pr(12_0002)=
$(1-T)(1-s)(e^{-M(t+2)})(1-e^{-qE_{24}})r_2[(1-e^{-m_{12}t})(e^{-q(E_{22}+E_{23})})+(e^{-m_{12}t-qE_{12}})(1-$
$e^{-m_{12}})(e^{-qE_{23}})+(e^{-m_{12}(t+1)-q(E_{12}+E_{13})})(1-e^{-m_{12}})]$

Pr(12_0000)= 1$-\sum(\mathrm{Pr_12_01}, \mathrm{Pr_12_001}, \mathrm{Pr_12_0001}, \mathrm{Pr_12_02}, \mathrm{Pr_12_002}, \mathrm{Pr_12_0002})$
Pr(22_01)=$(1-T)(1-s)(e^{-Mt})(1-e^{-m_{21}t})(1-e^{-qE_{12}})r_1$
Pr(22_001)=$(1-T)(1-s)(e^{-M(t+1)})(1-e^{-qE_{13}})r_1[(1-e^{-m_{21}t})(e^{-qE_{12}})+(e^{-m_{21}t-qE_{22}})(1-e^{-m_{21}})]$
Pr(22_0001)=
$(1-T)(1-s)(e^{-M(t+2)})(1-e^{-qE_{14}})r_1[(1-e^{-m_{21}t})(e^{-q(E_{12}+E_{13})})+(e^{-m_{21}t-qE_{22}})(1-$
$e^{-m_{21}})(e^{-qE_{13}})+(e^{-m_{21}(t+1)-q(E_{22}+E_{23})})(1-e^{-m_{21}})]$

Pr(22_02)=$(1-T)(1-s)(e^{-(M+m_{21})t})(1-e^{-qE_{22}})r_2$
Pr(22_002)=$(1-T)(1-s)(e^{-(M+m_{21})(t+1)-qE_{22}})(1-e^{-qE_{23}})r_2$

Pr(22_0002)=$(1-T)(1-s)\left(e^{-(M+m_{21})(t+2)-q(E_{22}+E_{23})}\right)(1-e^{-qE_{24}})r_2$
Pr(22_0000)= 1$-\sum($Pr_22_01, Pr_22_001, Pr_22_0001, Pr_22_02, Pr_22_002, Pr_22_0002$)$
Pr(13_001)=$(1-T)(1-s)\left(e^{-(M+m_{12})t}\right)(1-e^{-qE_{13}})r_1$
Pr(13_0001)=$(1-T)(1-s)\left(e^{-(M+m_{12})(t+1)-qE_{13}}\right)(1-e^{-qE_{14}})r_1$
Pr(13_002)=$(1-T)(1-s)(e^{-Mt})(1-e^{-m_{12}t})(1-e^{-qE_{23}})r_2$
Pr(13_0002)=$(1-T)(1-s)\left(e^{-M(t+1)}\right)(1-e^{-qE_{24}})r_2[(1-e^{-m_{12}t})(e^{-qE_{23}})+(e^{-m_{12}t-qE_{13}})(1-e^{-m_{12}})]$
Pr(13_0000)= 1$-\sum($Pr_13_001, Pr_13_0001, Pr_13_002, Pr_13_0002$)$
Pr(23_001)=$(1-T)(1-s)(e^{-Mt})(1-e^{-m_{21}t})(1-e^{-qE_{13}})r_1$
Pr(23_0001)=$(1-T)(1-s)\left(e^{-M(t+1)}\right)(1-e^{-qE_{14}})r_1[(1-e^{-m_{21}t})(e^{-qE_{13}})+(e^{-m_{21}t-qE_{23}})(1-e^{-m_{21}})]$
Pr(23_002)=$(1-T)(1-s)\left(e^{-(M+m_{21})t}\right)(1-e^{-qE_{23}})r_2$
Pr(23_0002)=$(1-T)(1-s)\left(e^{-(M+m_{21})(t+1)-qE_{23}}\right)(1-e^{-qE_{24}})r_2$
Pr(23_0000)= 1$-\sum($Pr_23_001, Pr_23_0001, Pr_23_002, Pr_23_0002$)$

APPENDIX 2. Statistical code for the capture-recapture model simulation in program R.

```
### PARAMETERS
M=0.7                              #NATURAL MORTALITY RATE
m12=0.05                           #MIGRATION RATE FROM REGION 1 TO REGION 2
m21=0.05                           #MIGRATION RATE FROM REGION 2 TO REGION 1
T=0.15                             #TAG MORTALITY RATE (DISCRETE)
s=0.05                             #TAG SHED RATE (DISCRETE)

#FLEET 1
q=0.0001                           #FLEET CATCHABILITY COEFFICIENT
r1=0.1                             #PROPORTION OF CATCH IN REGION 1 SCIENTIFICALLY OBSERVED FOR TAGS (OR FLEET REPORTING RATE REGION 1)
r2=0.1                             #PROPORTION OF CATCH IN REGION 2 SCIENTIFICALLY OBSERVED FOR TAGS (OR FLEET REPORTING RATE REGION 2)

E_min=3000
E_max=4000
E11=runif(1,E_min,E_max)           #FISHING EFFORT IN REGION 1 YEAR 1
E12=runif(1,E_min,E_max)           #FISHING EFFORT IN REGION 1 YEAR 2
E13=runif(1,E_min,E_max)           #FISHING EFFORT IN REGION 1 YEAR 3
E14=runif(1,E_min,E_max)           #FISHING EFFORT IN REGION 1 YEAR 4
E21=runif(1,E_min,E_max)           #FISHING EFFORT IN REGION 2 YEAR 1
E22=runif(1,E_min,E_max)           #FISHING EFFORT IN REGION 2 YEAR 2
E23=runif(1,E_min,E_max)           #FISHING EFFORT IN REGION 2 YEAR 3
E24=runif(1,E_min,E_max)           #FISHING EFFORT IN REGION 2 YEAR 4

#TAGGING EFFORT
N11=5000                           #NUMBER OF TAGGED FISH RELEASED IN REGION 1 YEAR 1
N12=N11                            #NUMBER OF TAGGED FISH RELEASED IN REGION 1 YEAR 2
N13=N11                            #NUMBER OF TAGGED FISH RELEASED IN REGION 1 YEAR 3
N21=N11                            #NUMBER OF TAGGED FISH RELEASED IN REGION 2 YEAR 1
N22=N11                            #NUMBER OF TAGGED FISH RELEASED IN REGION 2 YEAR 2
N23=N11                            #NUMBER OF TAGGED FISH RELEASED IN REGION 2 YEAR 3
PSAT1=200                          #NUMBER OF SATTELITE TAGGED FISH RELEASED IN REGION 1
PSAT2=200                          #NUMBER OF SATTELITE TAGGED FISH RELEASED IN REGION 2
PSAT_duration=6/12                 #SATTELITE TAG DURATION
Fish_held=500                      #NUMBER OF TAGGED FISH EXAMINED IN HANDLING STUDY
Reward1=500                        #NUMBER OF HIGH REWARD TAGGED FISH RELEASED IN REGION 1
Reward2=500                        #NUMBER OF HIGH REWARD TAGGED FISH RELEASED IN REGION 2
t=3/12                             #TIME BETWEEN TAGGING AND FISHING SEASONS


### Outcomes and Probabilities_Fish Tagged Year 1 in Region 1
theta=c(M,m12,m21,T,s,q,r1,r2,E11,E12,E13,E14,E21,E22,E23,E24)
CR_Pr11=function(theta)
{
M=theta[1]
m12=theta[2]
m21=theta[3]
T=theta[4]
s=theta[5]
q=theta[6]
r1=theta[7]
r2=theta[8]
E11=theta[9]
E12=theta[10]
E13=theta[11]
E14=theta[12]
E21=theta[13]
E22=theta[14]
E23=theta[15]
E24=theta[16]

### The first number indicates the region the fish was marked, the second indicates the study year, the string following represents the annual capture history
Pr_11_1=(1-T)*(1-s)*exp(-(M+m12)*t)*(1-exp(-q*E11))*r1
Pr_11_01=(1-T)*(1-s)*exp(-(M+m12)*(1+t)-q*E11)*(1-exp(-q*E12))*r1
Pr_11_001=(1-T)*(1-s)*exp(-(M+m12)*(2+t)-q*(E11+E12))*(1-exp(-q*E13))*r1
Pr_11_0001=(1-T)*(1-s)*exp(-(M+m12)*(3+t)-q*(E11+E12+E13))*(1-exp(-q*E14))*r1
Pr_11_2=(1-T)*(1-s)*exp(-M*t)*(1-exp(-m12*t))*(1-exp(-q*E21))*r2
Pr_11_02=(1-T)*(1-s)*exp(-M*(1+t))*(1-exp(-q*E22))*r2*((1-exp(-m12*t))*exp(-q*E21)+exp(-m12*t-q*E11)*(1-exp(-m12*1)))
Pr_11_002=(1-T)*(1-s)*exp(-M*(2+t))*(1-exp(-q*E23))*r2*((1-exp(-m12*t))*exp(-q*(E21+E22))+exp(-m12*t-q*(E11+E22))*(1-exp(-m12*1))+exp(-m12*(1+t)-q*(E11+E12))*(1-exp(-
m12*1)))
Pr_11_0002=(1-T)*(1-s)*exp(-M*(3+t))*(1-exp(-q*E24))*r2*((1-exp(-m12*t))*exp(-q*(E21+E22+E23))+exp(-m12*t-q*(E11+E22+E23))*(1-exp(-m12*1))+exp(-m12*(1+t)-
q*(E11+E12+E23))*(1-exp(-m12*1))+exp(-m12*(2+t)-q*(E11+E12+E13))*(1-exp(-m12*1)))
Pr_11_0000=                T+
                           (1-T)*s+
                           (1-T)*(1-s)*(
                           (1-exp(-M*t))+
                           exp(-(M+m12)*t)*(1-exp(-q*E11))*(1-r1)+
                           exp(-M*t)*(1-exp(-m12*t))*(1-exp(-q*E21))*(1-r2)+

                           exp(-(M+m12)*t-q*E11)*(1-exp(-M*1))+
                           exp(-M*t-q*E21)*(1-exp(-m12*t))*(1-exp(-M*1))+
                           exp(-(M+m12)*(t+1)-q*E11)*(1-exp(-q*E12))*(1-r1)+
                           exp(-M*(t+1)-q*E21)*(1-exp(-m12*t))*(1-exp(-q*E22))*(1-r2)+
                           exp(-M*(t+1)-m12*t-q*E11)*(1-exp(-m12*1))*(1-exp(-q*E22))*(1-r2)+

                           exp(-(M+m12)*(t+1)-q*(E11+E12))*(1-exp(-M*1))+
                           exp(-M*(t+1)-m12*t-q*(E11+E22))*(1-exp(-m12*1))*(1-exp(-M*1))+
                           exp(-M*(t+1)-q*(E21+E22))*(1-exp(-m12*t))*(1-exp(-M*1))+
                           exp(-(M+m12)*(t+2)-q*(E11+E12))*(1-exp(-q*E13))*(1-r1)+
                           exp(-M*(t+2)-q*(E21+E22))*(1-exp(-m12*t))*(1-exp(-q*E23))*(1-r2)+
                           exp(-M*(t+2)-m12*t-q*(E11+E22))*(1-exp(-m12*1))*(1-exp(-q*E23))*(1-r2)+
                           exp(-M*(t+2)-m12*(t+1)-q*(E11+E12))*(1-exp(-m12*1))*(1-exp(-q*E23))*(1-r2)+

                           exp(-(M+m12)*(t+2)-q*(E11+E12+E13))*(1-exp(-M*1))+
                           exp(-M*(t+2)-q*(E21+E22+E23))*(1-exp(-m12*t))*(1-exp(-M*1))+
                           exp(-M*(t+2)-m12*t-q*(E11+E22+E23))*(1-exp(-m12*1))*(1-exp(-M*1))+
                           exp(-M*(t+2)-m12*(t+1)-q*(E11+E12+E23))*(1-exp(-m12*1))*(1-exp(-M*1))+
                           exp(-(M+m12)*(t+3)-q*(E11+E12+E13+E14))+
                           exp(-(M+m12)*(t+3)-q*(E11+E12+E13))*(1-exp(-q*E14))*(1-r1)+
```

```
                        exp(-M*(t+3)-q*(E21+E22+E23+E24))*(1-exp(-m12*t))+
                        exp(-M*(t+3)-q*(E21+E22+E23))*(1-exp(-m12*t))*(1-exp(-q*E24))*(1-r2)+
                        exp(-M*(t+3)-m12*t-q*(E11+E22+E23+E24))*(1-exp(-m12*1))+
                        exp(-M*(t+3)-m12*t-q*(E11+E22+E23))*(1-exp(-m12*1))*(1-exp(-q*E24))*(1-r2)+
                        exp(-M*(t+3)-m12*(t+1)-q*(E11+E12+E23+E24))*(1-exp(-m12*1))+
                        exp(-M*(t+3)-m12*(t+1)-q*(E11+E12+E23))*(1-exp(-m12*1))*(1-exp(-q*E24))*(1-r2)+
                        exp(-M*(t+3)-m12*(t+2)-q*(E11+E12+E13+E24))*(1-exp(-m12*1))+
                        exp(-M*(t+3)-m12*(t+2)-q*(E11+E12+E13))*(1-exp(-m12*1))*(1-exp(-q*E24))*(1-r2)
                        )
probs11=c(Pr_11_1,Pr_11_01,Pr_11_001,Pr_11_0001,Pr_11_2,Pr_11_02,Pr_11_002,Pr_11_0002,Pr_11_0000)
probs11
}

### Outcomes and Probabilities_Fish Tagged Year 1 in Region 2
CR_Pr21=function(theta)
{
M=theta[1]
m12=theta[2]
m21=theta[3]
T=theta[4]
s=theta[5]
q=theta[6]
r1=theta[7]
r2=theta[8]
E11=theta[9]
E12=theta[10]
E13=theta[11]
E14=theta[12]
E21=theta[13]
E22=theta[14]
E23=theta[15]
E24=theta[16]

Pr_21_2=(1-T)*(1-s)*exp(-(M+m21)*t)*(1-exp(-q*E21))*r2
Pr_21_02=(1-T)*(1-s)*exp(-(M+m21)*(1+t)-q*E21)*(1-exp(-q*E22))*r2
Pr_21_002=(1-T)*(1-s)*exp(-(M+m21)*(2+t)-q*(E21+E22))*(1-exp(-q*E23))*r2
Pr_21_0002=(1-T)*(1-s)*exp(-(M+m21)*(3+t)-q*(E21+E22+E23))*(1-exp(-q*E24))*r2
Pr_21_1=(1-T)*(1-s)*exp(-M*t)*(1-exp(-m21*t))*(1-exp(-q*E11))*r1
Pr_21_01=(1-T)*(1-s)*exp(-M*(1+t))*(1-exp(-q*E12))*r1*((1-exp(-m21*t))*exp(-q*E11)+exp(-m21*t-q*E21)*(1-exp(-m21*1)))
Pr_21_001=(1-T)*(1-s)*exp(-M*(2+t))*(1-exp(-q*E13))*r1*((1-exp(-m21*t))*exp(-q*(E11+E12))+exp(-m21*t-q*(E21+E12))*(1-exp(-m21*1))+exp(-m21*(1+t)-q*(E21+E22))*(1-exp(-
m21*1)))
Pr_21_0001=(1-T)*(1-s)*exp(-M*(3+t))*(1-exp(-q*E14))*r1*((1-exp(-m21*t))*exp(-q*(E11+E12+E13))+exp(-m21*t-q*(E21+E12+E13))*(1-exp(-m21*1))+exp(-m21*(1+t)-
q*(E21+E22+E13))*(1-exp(-m21*1))+exp(-m21*(2+t)-q*(E21+E22+E23))*(1-exp(-m21*1)))
Pr_21_0000=             T+
                        (1-T)*s+
                        (1-T)*(1-s)*(
                        (1-exp(-M*t))+
                        exp(-(M+m21)*t)*(1-exp(-q*E21))*(1-r2)+
                        exp(-M*t)*(1-exp(-m21*t))*(1-exp(-q*E11))*(1-r1)+

                        exp(-(M+m21)*t-q*E21)*(1-exp(-M*1))+
                        exp(-M*t-q*E11)*(1-exp(-m21*t))*(1-exp(-M*1))+
                        exp(-(M+m21)*(t+1)-q*E21)*(1-exp(-q*E22))*(1-r2)+
                        exp(-M*(t+1)-q*E11)*(1-exp(-m21*t))*(1-exp(-q*E12))*(1-r1)+
                        exp(-M*(t+1)-m21*t-q*E21)*(1-exp(-m21*1))*(1-exp(-q*E12))*(1-r1)+

                        exp(-(M+m21)*(t+1)-q*(E21+E22))*(1-exp(-M*1))+
                        exp(-M*(t+1)-m21*t-q*(E21+E12))*(1-exp(-m21*1))*(1-exp(-M*1))+
                        exp(-M*(t+1)-q*(E11+E12))*(1-exp(-m21*t))*(1-exp(-M*1))+
                        exp(-(M+m21)*(t+2)-q*(E21+E22))*(1-exp(-q*E23))*(1-r2)+
                        exp(-M*(t+2)-q*(E11+E12))*(1-exp(-m21*t))*(1-exp(-q*E13))*(1-r1)+
                        exp(-M*(t+2)-m21*t-q*(E21+E12))*(1-exp(-m21*1))*(1-exp(-q*E13))*(1-r1)+
                        exp(-M*(t+2)-m21*(t+1)-q*(E21+E22))*(1-exp(-m21*1))*(1-exp(-q*E13))*(1-r1)+

                        exp(-(M+m21)*(t+2)-q*(E21+E22+E23))*(1-exp(-M*1))+
                        exp(-M*(t+2)-q*(E11+E12+E13))*(1-exp(-m21*t))*(1-exp(-M*1))+
                        exp(-M*(t+2)-m21*t-q*(E21+E12+E13))*(1-exp(-m21*1))*(1-exp(-M*1))+
                        exp(-M*(t+2)-m21*(t+1)-q*(E21+E22+E13))*(1-exp(-m21*1))*(1-exp(-M*1))+
                        exp(-(M+m21)*(t+3)-q*(E21+E22+E23+E24))+
                        exp(-(M+m21)*(t+3)-q*(E21+E22+E23))*(1-exp(-q*E24))*(1-r2)+
                        exp(-M*(t+3)-q*(E11+E12+E13+E14))*(1-exp(-m21*t))+
                        exp(-M*(t+3)-q*(E11+E12+E13))*(1-exp(-m21*t))*(1-exp(-q*E14))*(1-r1)+
                        exp(-M*(t+3)-m21*t-q*(E21+E12+E13+E14))*(1-exp(-m21*1))+
                        exp(-M*(t+3)-m21*t-q*(E21+E12+E13))*(1-exp(-m21*1))*(1-exp(-q*E14))*(1-r1)+
                        exp(-M*(t+3)-m21*(t+1)-q*(E21+E22+E13+E14))*(1-exp(-m21*1))+
                        exp(-M*(t+3)-m21*(t+1)-q*(E21+E22+E13))*(1-exp(-m21*1))*(1-exp(-q*E14))*(1-r1)+
                        exp(-M*(t+3)-m21*(t+2)-q*(E21+E22+E23+E14))*(1-exp(-m21*1))+
                        exp(-M*(t+3)-m21*(t+2)-q*(E21+E22+E23))*(1-exp(-m21*1))*(1-exp(-q*E14))*(1-r1)
                        )
probs21=c(Pr_21_1,Pr_21_01,Pr_21_001,Pr_21_0001,Pr_21_2,Pr_21_02,Pr_21_002,Pr_21_0002,Pr_21_0000)
probs21
}

### Outcomes and Probabilities_Fish Tagged Year 2 in Region 1
CR_Pr12=function(theta)
{
M=theta[1]
m12=theta[2]
m21=theta[3]
T=theta[4]
s=theta[5]
q=theta[6]
r1=theta[7]
r2=theta[8]
E11=theta[9]
E12=theta[10]
E13=theta[11]
E14=theta[12]
E21=theta[13]
E22=theta[14]
E23=theta[15]
```

```
E24=theta[16]

Pr_12_01=(1-T)*(1-s)*exp(-(M+m12)*t)*(1-exp(-q*E12))*r1
Pr_12_001=(1-T)*(1-s)*exp(-(M+m12)*(1+t)-q*E12)*(1-exp(-q*E13))*r1
Pr_12_0001=(1-T)*(1-s)*exp(-(M+m12)*(2+t)-q*(E12+E13))*(1-exp(-q*E14))*r1
Pr_12_02=(1-T)*(1-s)*exp(-M*t)*(1-exp(-m12*t))*(1-exp(-q*E22))*r2
Pr_12_002=(1-T)*(1-s)*exp(-M*(1+t))*(1-exp(-q*E23))*r2*((1-exp(-m12*t))*exp(-q*E22)+exp(-m12*t-q*E12)*(1-exp(-m12*1)))
Pr_12_0002=(1-T)*(1-s)*exp(-M*(2+t))*(1-exp(-q*E24))*r2*((1-exp(-m12*t))*exp(-q*(E22+E23))+exp(-m12*t-q*(E12+E23))*(1-exp(-m12*1))+exp(-m12*(1+t)-q*(E12+E13))*(1-
exp(-m12*1)))
Pr_12_0000=1-sum(Pr_12_01,Pr_12_001,Pr_12_0001,Pr_12_02,Pr_12_002,Pr_12_0002)
probs12=c(Pr_12_01,Pr_12_001,Pr_12_0001,Pr_12_02,Pr_12_002,Pr_12_0002,Pr_12_0000)
probs12
}

#Outcomes and Probabilities_Fish Tagged Year 2 in Region 2
CR_Pr22=function(theta)
{
M=theta[1]
m12=theta[2]
m21=theta[3]
T=theta[4]
s=theta[5]
q=theta[6]
r1=theta[7]
r2=theta[8]
E11=theta[9]
E12=theta[10]
E13=theta[11]
E14=theta[12]
E21=theta[13]
E22=theta[14]
E23=theta[15]
E24=theta[16]

Pr_22_01=(1-T)*(1-s)*exp(-M*t)*(1-exp(-m21*t))*(1-exp(-q*E12))*r1
Pr_22_001=(1-T)*(1-s)*exp(-M*(1+t))*(1-exp(-q*E13))*r1*((1-exp(-m21*t))*exp(-q*E12)+exp(-m21*t-q*E22)*(1-exp(-m21*1)))
Pr_22_0001=(1-T)*(1-s)*exp(-M*(2+t))*(1-exp(-q*E14))*r1*((1-exp(-m21*t))*exp(-q*(E12+E13))+exp(-m21*t-q*(E22+E13))*(1-exp(-m21*1))+exp(-m21*(1+t)-q*(E22+E23))*(1-
exp(-m21*1)))
Pr_22_02=(1-T)*(1-s)*exp(-(M+m21)*t)*(1-exp(-q*E22))*r2
Pr_22_002=(1-T)*(1-s)*exp(-(M+m21)*(1+t)-q*E22)*(1-exp(-q*E23))*r2
Pr_22_0002=(1-T)*(1-s)*exp(-(M+m21)*(2+t)-q*(E22+E23))*(1-exp(-q*E24))*r2
Pr_22_0000=1-sum(Pr_22_01,Pr_22_001,Pr_22_0001,Pr_22_02,Pr_22_002,Pr_22_0002)
probs22=c(Pr_22_01,Pr_22_001,Pr_22_0001,Pr_22_02,Pr_22_002,Pr_22_0002,Pr_22_0000)
probs22
}

#Outcomes and Probabilities_Fish Tagged Year 3 in Region 1
CR_Pr13=function(theta)
{
M=theta[1]
m12=theta[2]
m21=theta[3]
T=theta[4]
s=theta[5]
q=theta[6]
r1=theta[7]
r2=theta[8]
E11=theta[9]
E12=theta[10]
E13=theta[11]
E14=theta[12]
E21=theta[13]
E22=theta[14]
E23=theta[15]
E24=theta[16]

Pr_13_001=(1-T)*(1-s)*exp(-(M+m12)*t)*(1-exp(-q*E13))*r1
Pr_13_0001=(1-T)*(1-s)*exp(-(M+m12)*(1+t)-q*E13)*(1-exp(-q*E14))*r1
Pr_13_002=(1-T)*(1-s)*exp(-M*t)*(1-exp(-m12*t))*(1-exp(-q*E23))*r2
Pr_13_0002=(1-T)*(1-s)*exp(-M*(1+t))*(1-exp(-q*E24))*r2*((1-exp(-m12*t))*exp(-q*E23)+exp(-m12*t-q*E13)*(1-exp(-m12*1)))
Pr_13_0000=1-sum(Pr_13_001,Pr_13_0001,Pr_13_002,Pr_13_0002)
probs13=c(Pr_13_001,Pr_13_0001,Pr_13_002,Pr_13_0002,Pr_13_0000)
probs13
}

#Outcomes and Probabilities_Fish Tagged Year 3 in Region 2
CR_Pr23=function(theta)
{
M=theta[1]
m12=theta[2]
m21=theta[3]
T=theta[4]
s=theta[5]
q=theta[6]
r1=theta[7]
r2=theta[8]
E11=theta[9]
E12=theta[10]
E13=theta[11]
E14=theta[12]
E21=theta[13]
E22=theta[14]
E23=theta[15]
E24=theta[16]

Pr_23_001=(1-T)*(1-s)*exp(-M*t)*(1-exp(-m21*t))*(1-exp(-q*E13))*r1
Pr_23_0001=(1-T)*(1-s)*exp(-M*(t+1))*(1-exp(-q*E14))*r1*((1-exp(-m21*t))*exp(-q*E13)+exp(-m21*t-q*E23)*(1-exp(-m21*1)))
Pr_23_002=(1-T)*(1-s)*exp(-(M+m21)*t)*(1-exp(-q*E23))*r2
Pr_23_0002=(1-T)*(1-s)*exp(-(M+m21)*(t+1)-q*E23)*(1-exp(-q*E24))*r2
Pr_23_0000=1-sum(Pr_23_001,Pr_23_0001,Pr_23_002,Pr_23_0002)
probs23=c(Pr_23_001,Pr_23_0001,Pr_23_002,Pr_23_0002,Pr_23_0000)
```

```
probs23
}


#MODEL SIMULATION
trials=100
M_hats=vector(length=trials)
m12_hats=vector(length=trials)
m21_hats=vector(length=trials)
T_hats=vector(length=trials)
s_hats=vector(length=trials)
q_hats=vector(length=trials)
r1_hats=vector(length=trials)
r2_hats=vector(length=trials)

for(i in 1:trials)
                    {
                    E11=runif(1,E_min,E_max)
                    E12=runif(1,E_min,E_max)
                    E13=runif(1,E_min,E_max)
                    E14=runif(1,E_min,E_max)
                    E21=runif(1,E_min,E_max)
                    E22=runif(1,E_min,E_max)
                    E23=runif(1,E_min,E_max)
                    E24=runif(1,E_min,E_max)

                    theta=c(M,m12,m21,T,s,q,r1,r2,E11,E12,E13,E14,E21,E22,E23,E24)

                    #ELECTRONIC TAGGING
                    PSAT1_2=rbinom(1,PSAT1,1-exp(-m12*PSAT_duration))
                    PSAT2_1=rbinom(1,PSAT2,1-exp(-m21*PSAT_duration))
                    m12_hat=-log(1-PSAT1_2/PSAT1)/PSAT_duration
                    m21_hat=-log(1-PSAT2_1/PSAT2)/PSAT_duration

                    #HANDLING STUDY
                    Alive=rbinom(1,Fish_held,(1-T))
                    Alive_tagged=rbinom(1,Alive,(1-s))
                    T_hat=1-Alive/Fish_held
                    s_hat=1-Alive_tagged/Alive

                    #REPORTING STUDY
                    Rewards1=rmultinom(1,Reward1,c(CR_Pr11(theta)[1:4]/r1,CR_Pr11(theta)[5:8]/r2,1-sum(CR_Pr11(theta)[1:4]/r1,CR_Pr11(theta)[5:8]/r2)))[1:8]
                    Rewards2=rmultinom(1,Reward2,c(CR_Pr21(theta)[1:4]/r1,CR_Pr21(theta)[5:8]/r2,1-sum(CR_Pr21(theta)[1:4]/r1,CR_Pr21(theta)[5:8]/r2)))[1:8]

                    #SIMULATED RECAPTURE DATA
                    Returns11=rmultinom(1,N11,CR_Pr11(theta))[1:8]
                    Returns21=rmultinom(1,N21,CR_Pr21(theta))[1:8]
                    Returns12=rmultinom(1,N12,CR_Pr12(theta))[1:6]
                    Returns22=rmultinom(1,N22,CR_Pr22(theta))[1:6]
                    Returns13=rmultinom(1,N13,CR_Pr13(theta))[1:4]
                    Returns23=rmultinom(1,N23,CR_Pr23(theta))[1:4]

                    #Estimated reporting rates
                    r1_hat=(sum(Returns11)/N11)/(sum(Rewards1)/Reward1)
                    r2_hat=(sum(Returns21)/N21)/(sum(Rewards2)/Reward2)

                    #Parameter starting values
                    M_logit=-1
                    m12_logit=log(m12_hat/(1-m12_hat))
                    m21_logit=log(m21_hat/(1-m21_hat))
                    s_logit=log(s_hat/(1-s_hat))
                    T_logit=log(T_hat/(1-T_hat))
                    q_logit=-8
                    r1_logit=log(r1_hat/(1-r1_hat))
                    r2_logit=log(r2_hat/(1-r2_hat))

                    #LOG-LIKELIHOOD ESTIMATION
                    theta2=c(M_logit,q_logit)
                    MLE=function(theta2)
                              {
                              M=1/(1+exp(-theta2[1]))
                              m12=max(1/(1+exp(-m12_logit)),0.000001)
                              m21=max(1/(1+exp(-m21_logit)),0.000001)
                              s=max(1/(1+exp(-s_logit)),0.000001)
                              T=max(1/(1+exp(-T_logit)),0.000001)
                              q=1/(1+exp(-theta2[2]))
                              r1=max(1/(1+exp(-r1_logit)),0.000001)
                              r2=max(1/(1+exp(-r2_logit)),0.000001)

                              obs11=c(Returns11,N11-sum(Returns11))
                              obs21=c(Returns21,N21-sum(Returns21))
                              obs12=c(Returns12,N12-sum(Returns12))
                              obs22=c(Returns22,N22-sum(Returns22))
                              obs13=c(Returns13,N13-sum(Returns13))
                              obs23=c(Returns23,N23-sum(Returns23))

                              probs11=CR_Pr11(theta=c(M,m12,m21,T,s,q,r1,r2,E11,E12,E13,E14,E21,E22,E23,E24))
                              probs21=CR_Pr21(theta=c(M,m12,m21,T,s,q,r1,r2,E11,E12,E13,E14,E21,E22,E23,E24))
                              probs12=CR_Pr12(theta=c(M,m12,m21,T,s,q,r1,r2,E11,E12,E13,E14,E21,E22,E23,E24))
                              probs22=CR_Pr22(theta=c(M,m12,m21,T,s,q,r1,r2,E11,E12,E13,E14,E21,E22,E23,E24))
                              probs13=CR_Pr13(theta=c(M,m12,m21,T,s,q,r1,r2,E11,E12,E13,E14,E21,E22,E23,E24))
                              probs23=CR_Pr23(theta=c(M,m12,m21,T,s,q,r1,r2,E11,E12,E13,E14,E21,E22,E23,E24))

                              -sum(dmultinom(obs11,prob=probs11,log=T))-sum(dmultinom(obs21,prob=probs21,log=T))-sum(dmultinom(obs12,prob=probs12,log=T))-
sum(dmultinom(obs22,prob=probs22,log=T))-sum(dmultinom(obs13,prob=probs13,log=T))-sum(dmultinom(obs23,prob=probs23,log=T))
                              }

                    fit=optim(theta2,MLE)
                    fit

                    M_hats[i]=1/(1+exp(-fit$par[1]))
```

```
                    m12_hats[i]=m12_hat
                    m21_hats[i]=m21_hat
                    T_hats[i]=T_hat
                    s_hats[i]=s_hat
                    q_hats[i]=1/(1+exp(-fit$par[2]))
                    r1_hats[i]=r1_hat
                    r2_hats[i]=r2_hat
                    }

layout(matrix(c(0,1,2,0,3,4,0,5,6,0,7,8,0,0,0),nrow=5,ncol=3,byrow=T),widths=c(1,5,5),heights=c(5,5,5,5,1))
par(mai=c(0.3,0.1,0.2,0.1))
hist((M_hats-M)/M*100,col=8,xlim=c(-250,250),main='Natural Mortality',breaks=10)
hist((q_hats-q)/q*100,col=8,xlim=c(-250,250),main='Gear Catchability',breaks=10)
hist((m12_hats-m12)/m12*100,col=8,xlim=c(-250,250),main='Migration Region 1 to 2',breaks=10)
hist((m21_hats-m21)/m21*100,col=8,xlim=c(-250,250),main='Migration Region 2 to 1',breaks=10)
hist((s_hats-s)/s*100,col=8,xlim=c(-250,250),main='Tag Shedding',breaks=10)
hist((T_hats-T)/T*100,col=8,xlim=c(-250,250),main='Tagging Mortality',breaks=10)
hist((r1_hats-r1)/r1*100,col=8,xlim=c(-250,250),main='Reporting Rate Region 1',breaks=10)
hist((r2_hats-r2)/r2*100,col=8,xlim=c(-250,250),main='Reporting Rate Region 2',breaks=10)
mtext('Percent Bias',1,outer=TRUE,line=-2)

M_bias=mean((M_hats-M)/M)*100
LL_M_bias=quantile((M_hats-M)/M*100,0.025)
UL_M_bias=quantile((M_hats-M)/M*100,0.975)
M_CV=sd(M_hats)/mean(M_hats)
q_bias=mean((q_hats-q)/q)*100
LL_q_bias=quantile((q_hats-q)/q*100,0.025)
UL_q_bias=quantile((q_hats-q)/q*100,0.975)
q_CV=sd(q_hats)/mean(q_hats)
list(M_bias=M_bias,CI_M_bias=paste(round(LL_M_bias,0),"to",round(UL_M_bias,0)),M_CV=M_CV,q_bias=q_bias,CI_q_bias=paste(round(LL_q_bias,0),"to",round(UL_q_bias,0)),
q_CV=q_CV)

#results=cbind(M_hats,m12_hats,m21_hats,T_hats,s_hats,q_hats,r1_hats,r2_hats)
#write.csv(results,'C:/users/mlauretta/desktop/YFT_High.csv')
```