Working Paper C.3

Estimating instantaneous rates of regional migration and mortality from conventional tagging data

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Introduction

Movement of fish species among stock regions has long been known to occur, but treating stocks as separate closed systems when substantial net movement occurs could provide inaccurate inferences of stock demographic parameters and potentially assessment. For populations of migratory animals that may be subjected to different levels of mortality in various regions, migration rates among adjacent regions have been estimated through tag-recovery experiments (e.g. Hilborn 1990; Schwarz et al. 1993).

The statistical models for mark-recovery experiments usually consider release groups and recaptures made in discrete time where simplifying assumptions such as migration occurring only once and instantly between intervals and all tagged animals of a particular release group are released at the same time. Furthermore, many population dynamics models used to manage fisheries are parameterized with instantaneous mortality rates (e.g. Quinn and Deriso 1999) and it would appear natural to consider migration in the same continuous time framework.

A finite-state continuous-time approach for inferring instantaneous migration and mortality rates from different types of tagging studies including tag-recovery are the subject of recent work by Miller and Andersen (In review). Here we apply the statistical method to data from tag-recovery experiments by the Gulf of Maine Research Institute (GMRI) on Atlantic cod, but expand the set of states to allow estimation of tag reporting probabilities, tag shedding rates and account for incomplete mixing of newly released individuals.

The finite-state continuous-time model

A categorical characteristics of an individual that changes through time is a finite-state continuous-time (FSCT) stochastic process. The indication of the transition between categories and the times of these transitions is generally known as a counting process Andersen, Borgen, Gill, and Keiding (1993). Under certain assumptions, the parameters that characterize the counting processes for individuals of a population may be inferred through various tagging experiments (Miller and Andersen In review). These assumptions include those commonly made in tagging experiments: movement and mortality processes are the same for tagged and untagged animals and the processes for each animal are independent and Markovian. Because of the interval-censored observations provided by conventional tags, we further assume (piece-wise) homogeneous instantaneous rates of movement and mortality.

Atlantic cod example

The Gulf of Maine Research Institute (GMRI) released over 100,000 conventionally tagged Atlantic cod in the Gulf of Maine and other areas between 2003 and 2005. Some fish were released with either high or low-reward tags and some were released with 2 tags. Over 6000 individuals have been recovered to date, but we will consider the end of 2006 as the end-time of the study to reduce problems relating to delay of reporting recovered tags. We use the statistical modeling framework developed by Miller and Andersen (In review) with the times and regions of release and recovery, the type of tag (high-reward or low-reward) and the

number of tags for each tagged fish as data. The regions of interest are the Gulf of Maine, Georges Bank and the Canadian 4X area.

States of the process

When the kth tagged fish is released in one of three regions at time $t_{0,k}$ it may at any instant move to one of the other two regions or die due to fishing or natural causes (given fishing activities are occurring) or it may shed the tag and thereby remove itself from the study. If it is dies due to fishing at time $t_{r,k}$ in one of the three regions, it may be reported with probability $\rho < 1$. The tagged fish recovered may not be reported with probability $1 - \rho$. If the fish is released with two tags, each tag may at any instant shed as when there is a single tag, but one tag will still remain so that the fish remains in the study. The fish may also remain alive at the time of analysis t_a with 0, 1, or 2 tags, depending on how many it had at releaseAs such, there are 27 states that a double-tagged fish may exhibit and 18 states that a single-tagged fish may exhibit (Table 1).

The 27×27 instantaneous rate matrix is

$$\mathbf{A}_\tau = \begin{pmatrix} \boldsymbol{\mu}_{2,\tau} & 2L\mathbf{I} & \mathbf{0} & \boldsymbol{\rho}\mathbf{F}_\tau & \mathbf{0} & (\mathbf{I}-\boldsymbol{\rho})\mathbf{F}_\tau & \mathbf{0} & \mathbf{M} & \mathbf{0} \\ \mathbf{0} & \boldsymbol{\mu}_{1,\tau} & L\mathbf{I} & \mathbf{0} & \boldsymbol{\rho}\mathbf{F}_\tau & \mathbf{0} & (\mathbf{I}-\boldsymbol{\rho})\mathbf{F}_\tau & \mathbf{0} & \mathbf{M} \\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} \end{pmatrix}$$

where $\mathbf{I}$ is a 3×3 identity matrix and $\mathbf{0}$ is a 3×3 matrix of zeros in the first two rows and a 21×3 matrix of zeros, otherwise. The elements, $\mathbf{F}_\tau$ and $\mathbf{M}$ are 3×3 diagonal matrices of instantaneous tag-shedding ($(L_1, L_2, L_3)^T$), fishing ($(F_{1,\tau}, F_{2,\tau}, F_{3,\tau})^T$) and natural mortality rates ($(M_1, M_2, M_3)^T$), respectively, for regions 1-3, where $\tau \in \{2003, 2004, 2005, 2006\}$ indexes yearly time intervals. The 3×3 diagonal matrices $\boldsymbol{\rho}$ contains the three regional reporting probabilities ($(\rho_1, \rho_2, \rho_3)^T$) and L is the tag-shedding rate. For individuals released with low-reward tags, $0 < \rho_r < 1$, $r \in \{1, 2, 3\}$ and we assume $\rho_r = 1$ for high-reward tags. The remaining elements contain the instantaneous migration rates and forces of transition from the states along the diagonal,

$$\boldsymbol{\mu}_{2,\tau} = \begin{pmatrix} -a_{1,\tau} & \mu_{12} & \mu_{13} \\ \mu_{21} & -a_{2,\tau} & \mu_{23} \\ \mu_{31} & \mu_{32} & -a_{3,\tau} \end{pmatrix}$$

and

$$\boldsymbol{\mu}_{1,\tau} = \begin{pmatrix} -a_{4,\tau} & \mu_{12} & \mu_{13} \\ \mu_{21} & -a_{5,\tau} & \mu_{23} \\ \mu_{31} & \mu_{32} & -a_{6,\tau} \end{pmatrix}$$

where $a_{h,\tau}$ is the sum of the elements of $\mathbf{A}_\tau$ in row h off the diagonal. The doubling of tag-shedding rates for double-tagged fish implies that the shedding processes of each tag are independent and that the corresponding rates are equal (cf. Xiao 1996).

To allow for different fishing mortalities of tagged fish k between the time of release $t_{0,k}$ and 1 month later $t_{0,k} + 1/12$ we allow a modification to the fishing mortality matrices in $\mathbf{A}_\tau$. The instantaneous rate matrix for this period is

$$\mathbf{A}^*_\tau = \begin{pmatrix} \boldsymbol{\mu}_{2,\tau} & 2L\mathbf{I} & \mathbf{0} & \boldsymbol{\rho}\mathbf{F}^*_\tau & \mathbf{0} & (\mathbf{I}-\boldsymbol{\rho})\mathbf{F}^*_\tau & \mathbf{0} & \mathbf{M} & \mathbf{0} \\ \mathbf{0} & \boldsymbol{\mu}_{1,\tau} & L\mathbf{I} & \mathbf{0} & \boldsymbol{\rho}\mathbf{F}^*_\tau & \mathbf{0} & (\mathbf{I}-\boldsymbol{\rho})\mathbf{F}^*_\tau & \mathbf{0} & \mathbf{M} \\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} & \mathbf{0} \end{pmatrix}$$

where $\mathbf{F}^*_\tau = \boldsymbol{\gamma}\mathbf{F}_\tau$ and $\boldsymbol{\gamma}$ is a 3×3 diagonal matrices of region specific scalars ($(\gamma_1, \gamma_2, \gamma_3)^T$, $\gamma_r > 0$) to modify fishing mortality for the recent releases. Note that this allows fishing mortality for the first month to be either less than that of other fish ($0 < \gamma_r < 1$) or greater than that of other fish ($\gamma_r > 1$).

Models and likelihood

We considered a suite of nested models for the tagged cod populations in the 3 regions (Table 2). For the simplest (null) model we assume all migration rates are equal across regions and time, fishing mortality rates are equal across regions and time, reporting rates for the low-reward tags are equal across regions and time, tag-shedding rates are equal across regions and time and time and natural mortality rates are equal across regions and time ($M0$). For the next more complex model, we make the same assumptions except unobserved and observed fishing mortality rates are year-specific, but constant across regions ($M1$).

Let $Y_k(t) \in S = \{1, \ldots, h, \ldots, 27\}$ be the state tagged fish k is in at time $t_{0,k} \leq t \leq t_a$. Given a vector of unknown instantaneous rate parameters $\mathbf{a}$ in the instantaneous rate matrix, the likelihood we maximize is

$$\mathcal{L}(\mathbf{a}) = \left\{P_{Y_k(t_{0,k}),Y_k(t_{r,k}-)} a_{Y_k(t_{r,k}-),Y_k(t_{r,k})}\right\}^{I(Y_k(t_a)\in\mathcal{F})} \times \left\{\sum_{Y_k(t_{a,k})\notin\{\mathcal{F}\}}^{H} P_{Y_k(t_{0,k}),Y_k(t_a)}\right\}^{I(Y_k(t_a)\notin\{\mathcal{F}\})} \tag{1}$$

where $I(Y_k(t_a) \in \mathcal{F})$ is an indicator of whether the animal is in a caught and reported state at time of analysis and $I(Y_k(t_a) \notin \{\mathcal{F}\})$ is an indicator of whether the animal is any other state at time of analysis (Miller and Andersen In review, eq. 5). The first line in eq. 1 is the product of the probability of being alive in region of recovery just prior to capture at time $t_{r,k}-$ given $Y_k(t_{0,k})$ and the instantaneous rate of capture in the region where recovery occurred. The probability $P_{Y_k(t_{0,k}),Y_k(t_{r,k}-)}$ is the $(Y_k(t_{0,k}), Y_k(t_{r,k}-))$ element of the probability transition matrix, $\mathbf{P}(t_{0,k}, t_{r,k}-)$ and $a_{Y_k(t_{r,k}-),Y_k(t_{a,k})}$ is the $(Y_k(t_{r,k}-), Y_k(t_{a,k}))$ element of the instantaneous rate matrix ($\mathbf{A}_\tau$), such that $t_{r,k}$ is in the corresponding year. The second line in eq. 1 is the probability of being in any of the states not corresponding to capture and reporting at the time of analysis given $Y_k(t_{0,k})$ which is the sum of the elements of the probability transition matrix $\mathbf{P}(t_{0,k}, t_{a,k})$ in row $Y_k(t_{0,k})$ where $Y_k(t_{a,k}) \notin \{\mathcal{F}\}$. See (Miller and Andersen In review) for how the probability transition matrix is formed from the instantaneous rate matrix.

Model selection and parameter estimation

We used programs we wrote in `R` to evaluate and maximize log-likelihoods. We used the modified Newton-Raphson method available through the `optim` function for maximization and the numerically derived hessian matrix for variance estimation. To facilitate maximization the log-likelihood (i.e., avoid boundary constraints), we reparameterized the instantaneous rates as their logarithmic transformations and the reporting probabilities as their logit transformation.

For this paper, we have fit 4 nested models (Table 2). The null model (M_0) assumes all instantaneous rates, reporting probabilities and nonmixing scalars are constant across regions and years. The next model (M_1) relaxes the assumption of constant fishing mortality and nonmixing scalars across regions, model M_2 relaxes the assumption of constant fishing mortality across years and reporting probabilities across regions and the last model (M_3) relaxes the assumptions of constant migration rates across regions. We compare and determine a "best" model using likelihood ratio tests ($\alpha = 0.05$).

Results

The best of the 4 models we have considered so far (M_3) assumes migration rates to each of the other 2 regions from any given region are all different, fishing mortality rates are different between regions and across years and the reporting probabilities and nonmixing scalars differ between regions. The natural mortality rates and tag shedding rates are assumed constant across regions. The estimated fishing mortality rates were usually highest for the Canadian 4X region and lowest for the Georges Bank region (Table 3). The estimated nonmixing scalars indicate that fishing mortality of tagged fish is approximately 3, 1.7 and 2 times higher in the first month after release in the Gulf of Maine, Georges Bank and 4X regions, respectively. The estimated reporting probabilities indicate that about 70% of tagged fish recovered in the Georges Bank region were reported whereas only about 45 and 50% of recovered tags were reported in the Gulf of Maine and 4X regions, respectively. The estimated natural mortality rate was higher than we expected (approximately 0.64). The instantaneous migration rate estimates were most similar back and forth between the Gulf of Maine and 4X regions, but the movement from the 4X region to the George Bank region was large relative to the movement rate in the reverse direction (Figure 1). Movement rates between the Gulf of Maine and Georges Bank regions were larger than those between the the Gulf of Maine and 4X regions.

As would be expected, the MLEs for fishing mortality rates with and reporting rates in corresponding regions were strongly negatively correlated (Tables 4 and 5). Many fishing mortality rate estimates were strongly positively correlated with other fishing mortality rates for the same region but different years, but other MLEs (migration rates, natural mortality rate, tag shedding rate, non-mixing scalars) were not strongly correlated with any other MLEs.

Discussion

The main concern with the results so far is the unexpectedly high natural mortality rate. Potential causes for positive bias in natural mortality include 1) movement of fish to areas inaccessible to fishing or outside of the study area, 2) heterogeneity of size of released fish when there are differences in fishing mortality with size and 3) less than 100% reporting of high reward tags. The first potential cause is not readily dealt with using any tagging study, but the second cause could perhaps be treated by allowing fishing mortality to change with length and assuming a model for growth of tagged fish. Finally, the third cause is probably contributing substantially to the results here because tagged fish may just not be seen in large trawl catches. Unreporting of high-reward tags, does not appear to be a treatable

problem, but if we can assume that this occurs equally across regions, then although the natural mortality rate estimation would be positively biased, estimation of migration rates would be unbiased.

The 1-month period after release to allow for mixing of newly tagged individuals was an arbitrary decision for these preliminary results. The estimated fishing mortality multipliers (γ) were substantially different from 1 which would indicate that a longer mixing period after release may be more appropriate.

There are more biologically relevant models that we would like to consider in the future. For example, migration of cod is widely thought to be seasonal and this can be treated with the finite-state continuous-time approach by allowing quarterly adjustments from the yearly migration rate that are constant across years.

References

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Table 1. States a tagged Atlantic cod may exhibit during the time of the study.

State	Definition
1	Alive in the Gulf of Maine with 2 tags
2	Alive in the Georges Bank with 2 tags
3	Alive in the CAN4X with 2 tags
4	Alive in the Gulf of Maine with 1 tag
5	Alive in the Georges Bank with 1 tag
6	Alive in the CAN4X with 1 tag
7	Alive in the Gulf of Maine with 0 tags
8	Alive in the Georges Bank with 0 tags
9	Alive in the CAN4X with 0 tags
10	Caught in in the Gulf of Maine with 2 tags and reported
11	Caught in in the Georges Bank with 2 tags and reported
12	Caught in in the CAN4X with 2 tags and reported
13	Caught in in the Gulf of Maine with 1 tag and reported
14	Caught in in the Georges Bank with 1 tag and reported
15	Caught in in the CAN4X with 1 tag and reported
16	Caught in the Gulf of Maine with 2 tags and not reported
17	Caught in the Georges Bank with 2 tags and not reported
18	Caught in the CAN4X with 2 tags and not reported
19	Caught in the Gulf of Maine with 1 tag and not reported
20	Caught in the Georges Bank with 1 tag and not reported
21	Caught in the CAN4X with 1 tag and not reported
22	Dead from non-fishing causes in the Gulf of Maine with 2 tags
23	Dead from non-fishing causes in the Georges Bank with 2 tags
24	Dead from non-fishing causes in the CAN4X with 2 tags
25	Dead from non-fishing causes in the Gulf of Maine with 1 tag
26	Dead from non-fishing causes in the Georges Bank with 1 tag
27	Dead from non-fishing causes in the CAN4X with 1 tag

Table 2. Models considered in analyses.

Model	parameters	Loglikelihood	n_p	χ^2	P
M_0	μ, F, M, L, γ, ρ	-32628.91	6		
M_1	μ, M, L, ρ, γ_1, γ_2, γ_3 F_1, F_2, F_3	-32116.13	10	1025.565	< 0.0001
M_2	μ, M, L, ρ_1, ρ_2, ρ_3 γ_1, γ_2, γ_3 $F_{1,2003}$, $F_{2,2003}$, $F_{3,2003}$ $F_{1,2004}$, $F_{2,2004}$, $F_{3,2004}$ $F_{1,2005}$, $F_{2,2005}$, $F_{3,2005}$ $F_{1,2006}$, $F_{2,2006}$, $F_{3,2006}$	-31901.07	21	430.1122	< 0.0001
M_3	M, L, $\mu_{1,2}$, $\mu_{1,3}$, $\mu_{2,1}$, $\mu_{2,3}$, $\mu_{3,1}$, $\mu_{3,2}$ ρ_1, ρ_2, ρ_3 γ_1, γ_2, γ_3 $F_{1,2003}$, $F_{2,2003}$, $F_{3,2003}$ $F_{1,2004}$, $F_{2,2004}$, $F_{3,2004}$ $F_{1,2005}$, $F_{2,2005}$, $F_{3,2005}$ $F_{1,2006}$, $F_{2,2006}$, $F_{3,2006}$	-31832.95	26	136.24	< 0.0001

Table 3. Parameter estimates from model M_3.

Parameter	Estimate	SE
$\mu_{1,2}$	0.1567	0.0197
$\mu_{1,3}$	0.0341	0.0057
$\mu_{2,1}$	0.0966	0.0059
$\mu_{2,3}$	0.0434	0.0037
$\mu_{3,1}$	0.0688	0.0153
$\mu_{3,2}$	0.2331	0.0374
$F_{1,2003}$	0.1508	0.0153
$F_{2,2003}$	0.0370	0.0056
$F_{3,2003}$	0.2772	0.0402
$F_{1,2004}$	0.1289	0.0112
$F_{2,2004}$	0.0517	0.0075
$F_{3,2004}$	0.3388	0.0485
$F_{1,2005}$	0.1600	0.0135
$F_{2,2005}$	0.0505	0.0074
$F_{3,2005}$	0.1613	0.0272
$F_{1,2006}$	0.1709	0.0181
$F_{2,2006}$	0.0322	0.0053
$F_{3,2006}$	0.0588	0.0136
M	0.6419	0.0296
ρ_1	0.4570	0.0684
ρ_2	0.7222	0.2273
ρ_3	0.4949	0.1176
L	0.1494	0.0108
γ_1	3.0708	0.1895
γ_2	1.7094	0.1038
γ_3	2.0690	0.1815

Table 4. Estimated correlation of MLEs for migration rates, natural mortality rate, reporting probabilities and nonmixing scalars with all MLEs under model M_3.

	$\mu_{1,2}$	$\mu_{1,3}$	$\mu_{2,1}$	$\mu_{2,3}$	$\mu_{3,1}$	$\mu_{3,2}$	M	ρ_1	ρ_2	ρ_3	γ_1	γ_2	γ_3
$\mu_{1,2}$	1.00	−0.02	−0.11	−0.03	−0.02	0.00	−0.12	0.03	0.03	−0.04	−0.12	0.08	0.01
$\mu_{1,3}$	−0.02	1.00	−0.03	0.11	−0.04	−0.09	−0.02	−0.01	0.00	0.05	−0.04	0.00	0.09
$\mu_{2,1}$	−0.11	−0.03	1.00	0.03	−0.02	−0.03	0.12	−0.03	−0.03	0.02	0.13	−0.09	−0.01
$\mu_{2,3}$	−0.03	0.11	0.03	1.00	−0.08	−0.12	0.02	0.01	−0.02	0.06	−0.01	−0.04	0.14
$\mu_{3,1}$	−0.02	−0.04	−0.02	−0.08	1.00	−0.01	0.03	−0.01	0.00	0.01	0.04	−0.01	−0.07
$\mu_{3,2}$	0.00	−0.09	−0.03	−0.12	−0.01	1.00	−0.02	−0.01	0.00	0.16	0.01	0.05	−0.13
M	−0.12	−0.02	0.12	0.02	0.03	−0.02	1.00	0.22	0.18	0.24	−0.16	−0.22	−0.07
ρ_1	0.03	−0.01	−0.03	0.01	−0.01	−0.01	0.22	1.00	0.04	0.05	0.10	−0.05	−0.01
ρ_2	0.03	0.00	−0.03	−0.02	0.00	0.00	0.18	0.04	1.00	0.05	−0.04	0.03	−0.01
ρ_3	−0.04	0.05	0.02	0.06	0.01	0.16	0.24	0.05	0.05	1.00	−0.04	−0.05	0.17
γ_1	−0.12	−0.04	0.13	−0.01	0.04	0.01	−0.16	0.10	−0.04	−0.04	1.00	0.03	0.01
γ_2	0.08	0.00	−0.09	−0.04	−0.01	0.05	−0.22	−0.05	0.03	−0.05	0.03	1.00	0.01
γ_3	0.01	0.09	−0.01	0.14	−0.07	−0.13	−0.07	−0.01	−0.01	0.17	0.01	0.01	1.00
$F_{1,2003}$	0.04	0.03	−0.06	0.00	−0.02	0.01	−0.10	−0.79	−0.01	−0.02	−0.39	0.03	0.01
$F_{2,2003}$	−0.05	0.00	0.05	0.03	0.00	−0.01	−0.10	−0.02	−0.94	−0.03	0.03	−0.15	0.01
$F_{3,2003}$	0.03	−0.09	−0.02	−0.13	0.03	−0.06	−0.17	−0.04	−0.03	−0.90	0.03	0.04	−0.39
$F_{1,2004}$	0.08	0.04	−0.09	0.00	−0.03	0.00	−0.04	−0.84	0.01	−0.01	−0.33	0.02	0.01
$F_{2,2004}$	−0.07	0.00	0.07	0.04	0.00	−0.02	−0.07	−0.01	−0.97	−0.02	0.03	−0.14	0.01
$F_{3,2004}$	0.02	−0.15	−0.01	−0.21	0.07	0.03	−0.10	−0.02	−0.02	−0.90	0.02	0.03	−0.30
$F_{1,2005}$	0.13	0.06	−0.12	0.00	−0.03	0.00	0.07	−0.81	0.03	0.02	−0.28	−0.01	0.00
$F_{2,2005}$	−0.10	0.00	0.10	0.05	0.00	−0.03	0.02	0.01	−0.95	0.00	0.02	−0.09	0.00
$F_{3,2005}$	0.01	−0.22	0.00	−0.32	0.11	0.12	0.01	0.00	0.00	−0.77	0.01	0.01	−0.25
$F_{1,2006}$	0.19	0.08	−0.14	0.01	−0.04	−0.01	0.27	−0.66	0.06	0.07	−0.24	−0.05	−0.01
$F_{2,2006}$	−0.16	0.00	0.14	0.07	0.01	−0.05	0.18	0.04	−0.84	0.04	−0.01	−0.12	−0.01
$F_{3,2006}$	−0.01	−0.22	0.02	−0.30	0.11	0.15	0.11	0.02	0.01	−0.52	−0.01	−0.02	−0.20
L	0.00	0.00	0.01	0.00	0.00	0.00	−0.37	−0.02	−0.01	−0.01	0.01	0.01	0.00

Table 5. Estimated correlation of MLEs for fishing mortality rates and tag shedding rate with all MLEs under model M_3.

	$F_{1,2003}$	$F_{2,2003}$	$F_{3,2003}$	$F_{1,2004}$	$F_{2,2004}$	$F_{3,2004}$	$F_{1,2005}$	$F_{2,2005}$	$F_{3,2005}$	$F_{1,2006}$	$F_{2,2006}$	$F_{3,2006}$	L
$\mu_{1,2}$	0.04	−0.05	0.03	0.08	−0.07	0.02	0.13	−0.10	0.01	0.19	−0.16	−0.01	0.00
$\mu_{1,3}$	0.03	0.00	−0.09	0.04	0.00	−0.15	0.06	0.00	−0.22	0.08	0.00	−0.22	0.00
$\mu_{2,1}$	−0.06	0.05	−0.02	−0.09	0.07	−0.01	−0.12	0.10	0.00	−0.14	0.14	0.02	0.01
$\mu_{2,3}$	0.00	0.03	−0.13	0.00	0.04	−0.21	0.00	0.05	−0.32	0.01	0.07	−0.30	0.00
$\mu_{3,1}$	−0.02	0.00	0.03	−0.03	0.00	0.07	−0.03	0.00	0.11	−0.04	0.01	0.11	0.00
$\mu_{3,2}$	0.01	−0.01	−0.06	0.00	−0.02	0.03	0.00	−0.03	0.12	−0.01	−0.05	0.15	0.00
M	−0.10	−0.10	−0.17	−0.04	−0.07	−0.10	0.07	0.02	0.01	0.27	0.18	0.11	−0.37
ρ_1	−0.79	−0.02	−0.04	−0.84	−0.01	−0.02	−0.81	0.01	0.00	−0.66	0.04	0.02	−0.02
ρ_2	−0.01	−0.94	−0.03	0.01	−0.97	−0.02	0.03	−0.95	0.00	0.06	−0.84	0.01	−0.01
ρ_3	−0.02	−0.03	−0.90	−0.01	−0.02	−0.90	0.02	0.00	−0.77	0.07	0.04	−0.52	−0.01
γ_1	−0.39	0.03	0.03	−0.33	0.03	0.02	−0.28	0.02	0.01	−0.24	−0.01	−0.01	0.01
γ_2	0.03	−0.15	0.04	0.02	−0.14	0.03	−0.01	−0.09	0.01	−0.05	−0.12	−0.02	0.01
γ_3	0.01	0.01	−0.39	0.01	0.01	−0.30	0.00	0.00	−0.25	−0.01	−0.01	−0.20	0.00
$F_{1,2003}$	1.00	0.00	0.01	0.76	−0.01	0.01	0.72	−0.01	0.00	0.60	−0.03	−0.01	0.01
$F_{2,2003}$	0.00	1.00	0.02	−0.01	0.93	0.01	−0.02	0.91	0.00	−0.04	0.82	0.00	0.01
$F_{3,2003}$	0.01	0.02	1.00	0.00	0.01	0.87	−0.02	−0.01	0.75	−0.05	−0.03	0.53	0.01
$F_{1,2004}$	0.76	−0.01	0.00	1.00	−0.01	0.00	0.79	−0.02	−0.01	0.69	−0.02	−0.01	0.01
$F_{2,2004}$	−0.01	0.93	0.01	−0.01	1.00	0.00	−0.02	0.95	0.00	−0.03	0.87	0.00	0.00
$F_{3,2004}$	0.01	0.01	0.87	0.00	0.00	1.00	−0.02	−0.01	0.83	−0.04	−0.02	0.60	0.00
$F_{1,2005}$	0.72	−0.02	−0.02	0.79	−0.02	−0.02	1.00	−0.02	−0.01	0.76	−0.01	0.00	0.00
$F_{2,2005}$	−0.01	0.91	−0.01	−0.02	0.95	−0.01	−0.02	1.00	0.00	−0.01	0.89	0.01	0.00
$F_{3,2005}$	0.00	0.00	0.75	−0.01	0.00	0.83	−0.01	0.00	1.00	−0.01	0.00	0.62	0.00
$F_{1,2006}$	0.60	−0.04	−0.05	0.69	−0.03	−0.04	0.76	−0.01	−0.01	1.00	0.03	0.02	−0.02
$F_{2,2006}$	−0.03	0.82	−0.03	−0.02	0.87	−0.02	−0.01	0.89	0.00	0.03	1.00	0.03	−0.01
$F_{3,2006}$	−0.01	0.00	0.53	−0.01	0.00	0.60	0.00	0.01	0.62	0.02	0.03	1.00	−0.01
L	0.01	0.01	0.01	0.01	0.00	0.00	0.00	0.00	0.00	−0.02	−0.01	−0.01	1.00

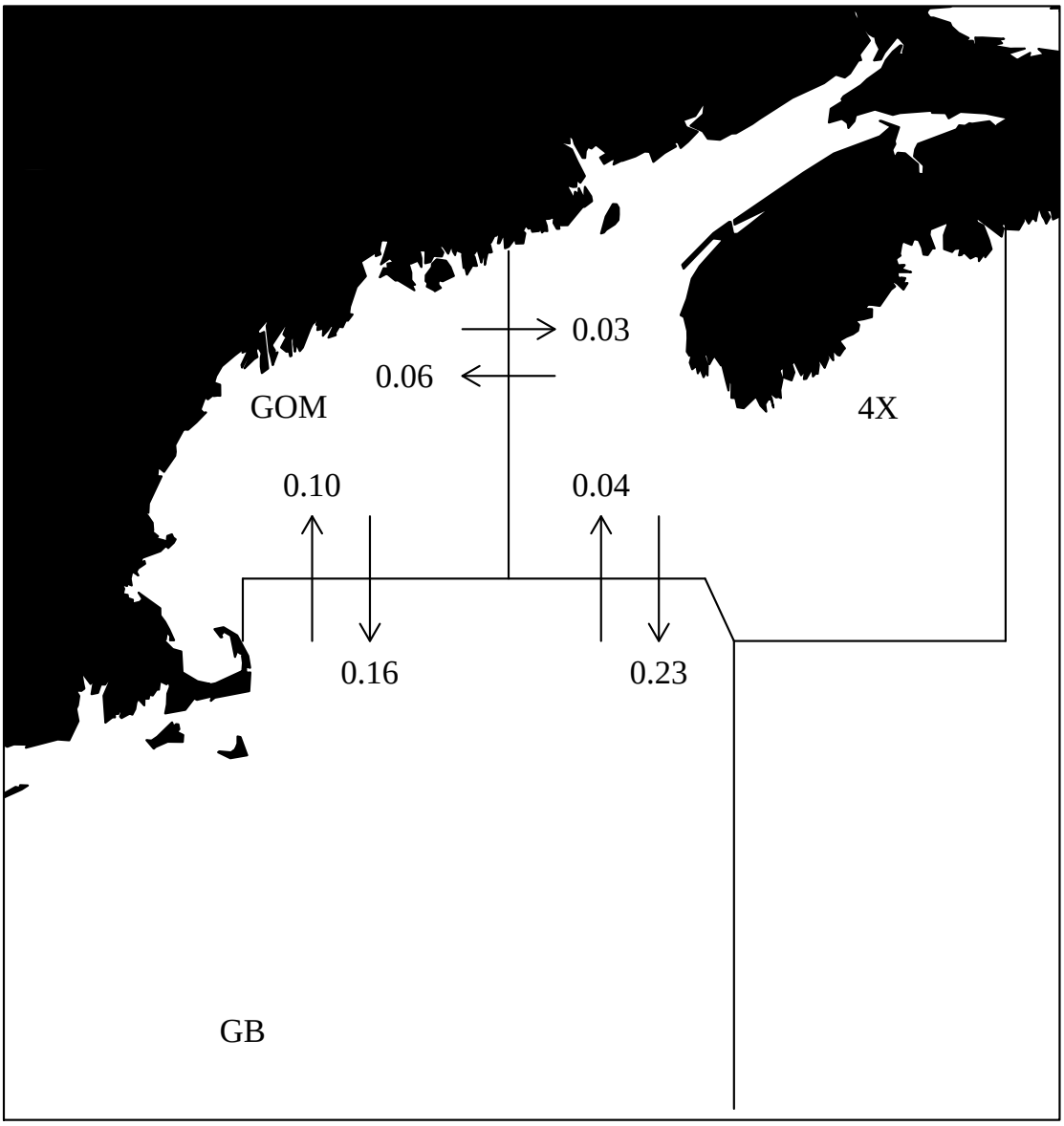

Figure 1. Regional instantaneous migration rates estimated from model M_3 (see Table 2).