Markov Chains and Leslie Matrix in Analytica

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The class of mathematical processes characterized by dynamic dependencies between successive random variables is called Markov chains. The rich behavior and wide applicability of Markov chains make them important in a variety of applied mathematical applications including population and demographics, health outcomes, marketing, genetics, and renewable resources. Analytica's dynamic modeling capabilities, robust array handling, and flexible uncertainty capabilities support sophisticated Markov modeling. In this webinar, a Markov modeling application is demonstrated. The model develops age-structured population simulations using a Leslie matrix structure and dynamic simulation in Analytica.

Age-structured population models provide the quantitative framework for the representation of populations. Such models are commonly used for analysis of human demographics (Pollard 1973) and renewable resources (Getz and Haight 1989). With respect to fisheries, Leslie (1945) developed the representation of a linear discrete population model as a matrix equation: this representation is now commonly referred to as the Leslie matrix population model. This model is commonly used in fisheries management and has been an important component of best professional judgment (BPJ) 316(b) assessments under 1977 draft guidance (Akçakaya, Burgman, and Ginzburg 2002; Public Service Electric and Gas Company [PSEG] 1999; U.S. Environmental Protection Agency [EPA] 2002).[1]

The mathematical representation of the Leslie matrix is:

[1] Fishery managers use the Leslie matrix in various applications. For example, the Shark Population Assessment Group of the National Oceanic and Atmospheric Administration (2006) uses the Leslie matrix to represent the population dynamics of sharks through demographic methods and to assess the status of shark stocks through stock assessment methodology. Sabaton et al. use a mathematical model to represent long-term change in a trout population under different river management scenarios. Their model describes the structure of a population divided into age classes based on the Leslie matrix. Hein et al. (2006) use an age-structured Leslie matrix model to determine which removal method most effectively reduced the population of invasive rusty crayfish in an isolated lake in Wisconsin. Carlson, Cortés, and Bethea (2003) simulated Leslie matrices to study the life history and population dynamics of the finetooth shark in the northeastern Gulf of Mexico.

$$\underbrace{\begin{pmatrix} N_{1,t+1} \\ N_{2,t+1} \\ N_{3,t+1} \\ \vdots \\ N_{A,t+1} \end{pmatrix}}_{\text{Estimated Population at Time } t+1} = \underbrace{\left(\begin{array}{cccc} \multicolumn{4}{c}{\overbrace{S_0 f_1 \quad S_0 f_2 \quad \cdots \quad S_0 f_A}^{\text{Fecundity}}} \\ S_1 & 0 & \cdots & 0 \\ 0 & S_2 & 0\ldots & 0 \\ \vdots & 0 & \vdots & \vdots \\ 0 & \cdots & S_{A-1} & 0 \end{array}\right)}_{\text{Transition Matrix}} \underbrace{\begin{pmatrix} N_{1,t} \\ N_{2,t} \\ N_{3,t} \\ \vdots \\ N_{A,t} \end{pmatrix}}_{\text{Initial Population at Time } t} \tag{3.1}$$

This representation consists of a population vector and a transition matrix.

$N_1...N_A$ is the population vector. The population vector represents the stage-structural population of a single stock at time t. Using a population of yellow perch as an example, $N_{1,t}$ would be the number of Age-1 yellow perch in the population at time t, $N_{2,t}$ would be the number of Age-2's in the population at time t, through all the lifestages for yellow perch.

As the equality condition indicates, multiplying the age-structured population vector at time t by the transition matrix returns the age-structured population vector at time t + 1. Thus, with knowledge of a population's structure and the transition matrix, it is possible to predict the population's structure in the next time period. Proceeding in a recursive way allows simulation of populations for future periods.

This type of model is an important tool for the quantitative assessment of I&E impacts. The next section describes the role of survival rates in a Leslie matrix and provides an example of how those rates can be calculated using life history tables such as compiled by EPA during Phase II rulemaking.

1.1 Survival Rates in Population Modeling

Survival rates in the transition matrix represent the probabilities that a fish in a population will survive to the next life-stage. The transition matrix is constructed so that the number in a specific cell is the probability an age-class member will survive to the next age-class. In Figure 1 below, Age 1's will have a 0.0697 probability of surviving to become Age 2's. Applied at the population level, these survival probabilities are the percentage of one life-stage that survives to the next. The survival rates between life-stages can be calculated from available life-history tables.

	Age 1+	Age 2+	Age 3+	Age 4+	Age 5+	Age 6+	Age 7+
Age 1+	0	0	0	0	0	0	0
Age 2+	0.696979	0	0	0	0	0	0
Age 3+	0	0.77958	0	0	0	0	0
Age 4+	0	0	0.2999918	0	0	0	0
Age 5+	0	0	0	0.2999918	0	0	0
Age 6+	0	0	0	0	0.2999918	0	0
Age 7+	0	0	0	0	0	0.2999918	0

Figure 1: A Basic Leslie Transition Matrix with Survival Probabilities

When a population at time t is multiplied by the above transition matrix (Equation 3.1), a proportion of the Age1's will survive the year and transition to Age2's at time t+1. Using natural and fishing mortality parameters from EPA, the survival rate can be calculated for each life-stage transition using Baranov's catch equation:

$$\text{Survival (S)} = \exp \text{^}{-}(M + F) \qquad \textbf{(3.2)}$$

The following example demonstrates how to calculate the survival rate (S) for the transition from an Age 3 yellow perch to an Age 4 using mortality values from EPA mortality tables: the Age 3 to Age 4 transition is used as an example because this is the earliest life-stage of yellow perch that includes fishing mortality.

$$\text{Survival (S)} = e \text{ ^ } - (0.844 + 0.36) = 0.2999 \qquad \textbf{(3.3)}$$

1.2 Mortality and Harvesting in Population Modeling

In addition to the age-structured population of survivors, it is also possible to structure the transition matrix to provide a decomposition of the death outcomes. The survival rate can be used to calculate the overall death rate for each life-stage, which can be decomposed to provide death rates due to fishing or natural causes. These rates can be used to project fishing and natural mortality over each life-stage as the population breakdown is expanded over the years' of the population's life. The fishing mortality rate can be further decomposed to identify the fish caught commercially or recreationally. These rates can be used to project commercial and recreational catch.

Total Death Rate = 1 – Total Survival Rate **(3.4)**
Natural Death Rate = M/(M+F) * Total Death Rate **(3.5)**
Fishing Death Rate = F/(M+F) * Total Death Rate **(3.6)**
*Commercial Death Rate = % of Commercial Fishing Mortality * Fishing Death rate **(3.7)**
*Recreational Death Rate = (1 – % of Commercial Fishing Mortality) * Fishing Death rate **(3.8)**

Using Age 3 yellow perch as an example, the outcome probabilities are:

Total Survival Rate	=	$e^{-(0.844 + 0.36)}$	= 0.2999	**(3.9)**
Total Death Rate	=	1 – 0.300	= 0.7001	**(3.10)**
Natural Death Rate	=	0.844/1.204 * 0.700	= 0.4907	**(3.11)**
Fishing Death Rate	=	0.36/1.204 * 0.700	= 0.2093	**(3.12)**
Comm. Death Rate	=	0.5 * Fishing Death rate	= 0.1046	**(3.13)**
Recr. Death Rate	=	0.5 * Fishing Death rate	= 0.1046	**(3.14)**

Outcome probabilities above match the Age 3 column of the transition matrix shown in Figure 2.

	Age 1+	Age 2+	Age 3+	Age 4+	Age 5+	Age 6+	Age 7+
Age 1+	0	0	0	0	0	0	0
Age 2+	0.696979	0	0	0	0	0	0
Age 3+	0	0.77958	0	0	0	0	0
Age 4+	0	0	0.2999918	0	0	0	0
Age 5+	0	0	0	0.2999918	0	0	0
Age 6+	0	0	0	0	0.2999918	0	0
Age 7+	0	0	0	0	0	0.2999918	0
Count Caught Rec	0	0	0.1046524	0.1046524	0.1046524	0.1046524	0
Count Caught Comm	0	0	0.1046524	0.1046524	0.1046524	0.1046524	0
Count Died Naturally	0.303021	0.22042	0.4907034	0.4907034	0.4907034	0.4907034	0
Totals	1	1	1	1	1	1	0

Figure 2: A Leslie Transition Matrix with Possible Mortality Outcome Probabilities

The fishing mortality has two components; fish that are caught recreationally and fish that are caught commercially. When there is specific data to support a ratio of recreational or commercial mortality within the overall fishing mortality (i.e., recreational mortality makes up 33 percent of the overall fishing mortality), this ratio is applied to the fishing death rate to calculate the recreational and commercial death rates. If no specific ratio data is available, the fishing mortality is equally divided between commercial mortality and recreational.

Like the survival-only transition matrix, the Age 3 column of the matrix contains the probabilities that an Age 3 fish will transition to another "state" as time transitions from t to t+1. The difference is that these possible transitions include outcomes that remove the fish from the population in the subsequent years (fish died naturally, fish caught recreationally, fish caught commercially, etc.).

1.3 Setup of the Transition Matrix

To begin setting up the transition matrix, begin with a chance node and set it up to be an edit table indexed by the lifestages in the T and T+1 indexes.

The nodes that compute the transition rates (i.e., commercial death rate, survival rate, etc.) do so across all the lifestage transitions in index T. The evaluation of the commercial death rate node for yellow perch is shown below.

Age 1+	0
Age 2+	0
Age 3+	0.1047
Age 4+	0.1047
Age 5+	0.1047
Age 6+	0.1047

The value in each cell is the probability that a fish at the lifestage at the T index column will transition to state described by the T+1 row index. So, the appropriate transition probability is filled into the transition table as shown below.

Edit Table of YPerch Transition Rates

YPerch T+1 / YPerch T

	Age 1+	Age 2+	Age 3+	Age 4+
Age 1+	1	0	0	
Age 2+	Yperch_survival_rate[Yperch_mort_rows='Age 1+']	0	0	
Age 3+	0	Yperch_survival_rate[Yperch_mort_rows='Age 2+']	0	
Age 4+	0	0	Yperch_survival_rate[Yperch_mort_rows='Age 3+']	
Age 5+	0	0	0	Yperch_survival_rate[Ype
Age 6+	0	0	0	
Age 7+	0	0	0	
Count Caught Rec	Yperch_rec_death_rat[Yperch_mort_rows='Age 1+']	Yperch_rec_death_rat[Yperch_mort_rows='Age 2+']	Yperch_rec_death_rat[Yperch_mort_rows='Age 3+']	Yperch_rec_death_rat[Ype
Count Caught Comm	Yperch_comm_death_ra[Yperch_mort_rows='Age 1+']	Yperch_comm_death_ra[Yperch_mort_rows='Age 2+']	Yperch_comm_death_ra[Yperch_mort_rows='Age 3+']	Yperch_comm_death_ra[Ype
Count Died Naturally	Yperch_nat_death_rat[Yperch_mort_rows='Age 1+']	Yperch_nat_death_rat[Yperch_mort_rows='Age 2+']	Yperch_nat_death_rat[Yperch_mort_rows='Age 3+']	Yperch_nat_death_rat[Ype

1.4 Utilization of the Transition Matrix

The purpose of this transition matrix is to operate on an initial population and project how the population will transition (survive, be caught commercially, etc.) over the years of the simulation.

The dynamic expansion of the population is accomplished using the dynamic function, where an initial population vector (a table indexed by T) is expanded over the years of the simulation using the following node definition.

Dynamic(Yperch_initial_popul, Slice (Sum (Self[Time-1]*Yperch_transition_ra, Yperch_t), Yperch_t_1, cumulate(1,Yperch_t)))

Figure 3 represents the expansion of a 2007 yellow perch population of 1000 Age 1's, 50 Age 2's, and 10 Age 4's. The transition matrix from Figure 2 is used to expand the population vector over time (years).

	2007	2008	2009	2010	2011	2012	2013	2014
Age 1+	1000	0	0	0	0	0	0	0
Age 2+	50	696.979	0	0	0	0	0	0
Age 3+	0	38.979	543.3509	0	0	0	0	0
Age 4+	10	0	11.69338	163.0008	0	0	0	0
Age 5+	0	2.999918	0	3.507919	48.89892	0	0	0
Age 6+	0	0	0.899951	0	1.052347	14.66928	0	0
Age 7+	0	0	0	0.269978	0	0.3156955	4.400663	0
Count Caught Rec	0	1.046524	4.393194	58.18089	17.42554	5.227519	1.535175	0
Count Caught Comm	0	1.046524	4.393194	58.18089	17.42554	5.227519	1.535175	0
Count Died Naturally	0	318.949	174.2273	272.8037	81.70641	24.51126	7.198264	0

Figure 3: Example of an Age-Structured Population Starting in 2007

1.5 Regeneration in Population Modeling

A population regenerates by spawning. Regeneration can be represented in the transition matrix by including stage-specific fecundity in the top row. The top row of the transition matrix represents the number of Age 1's expected from the spawn of mature adults. It is the product of the number of eggs a female in that age-class is expected to lay and the number of Age 1's expected from each egg.

	Age 1+	Age 2+	Age 3+	Age 4+	Age 5+	Age 6+	Age 7+
Age 1+	0	0	0	4.951804	4.951804	4.951804	0
Age 2+	0.696979	0	0	0	0	0	0
Age 3+	0	0.77958	0	0	0	0	0
Age 4+	0	0	0.2999918	0	0	0	0
Age 5+	0	0	0	0.2999918	0	0	0
Age 6+	0	0	0	0	0.2999918	0	0
Age 7+	0	0	0	0	0	0.2999918	0

Figure 4: Leslie Transition Matrix with Regeneration

From www.FishBase.org, the fecundity of Yellow Perch for each mature adult (Age 4 and above) is expected to lay 18,189 eggs. Using mortality values from EPA, the number of Age 1's which survive from each egg is 0.0002722.

18,189 eggs from each mature female * 0.0002722 Age1's from each egg = 4.95 Age1's **(3.15)**

For all lifestages Age 4 and older, each female is expected to generate 4.95 Age 1's in the next year.

Figure 5 represents the expansion of a 2007 yellow perch population of 1,000 Age 1's, 50 Age 2's, and 10 Age 4's. The transition matrix from Figure 4 is used to expand the population vector over time (years).

	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016
Age 1+	1000	49.51804	14.85501	62.35971	824.5186	287.3172	96.61976	57.52744	681.6873	436.0845
Age 2+	50	696.979	34.51303	10.35363	43.46341	574.6722	200.2541	67.34194	40.09542	475.1218
Age 3+	0	38.979	543.3509	26.90567	8.071481	33.8832	448.0029	156.1141	52.49843	31.25758
Age 4+	10	0	11.69338	163.0008	8.071481	2.421378	10.16468	134.3972	46.83295	15.7491
Age 5+	0	2.999918	0	3.507919	48.89892	2.421378	0.7263938	3.049322	40.31807	14.0495
Age 6+	0	0	0.899951	0	1.052347	14.66928	0.7263938	0.2179122	0.9147718	12.09509
Age 7+	0	0	0	0.269978	0	0.3156955	4.400663	0.2179122	0.06537188	0.2744241

Figure 5: A Population Expanded over Time with Regeneration

1.6 Biomass vs. Number of Organisms as Effectiveness Metrics

In certain measurements of population-level fishery impacts, the biomass of fish caught is a better valuation than the number of organisms caught.

In order to expand the Leslie transition matrix to allow biomass calculations, the probability of a certain outcome for a lifestage is multiplied by the average weight at that lifestage (available by lifestage from same table as natural (M) and fishing (F) mortality) when building the probabilities for the transition matrix. This will enable the matrix to calculate biomass by lifestage from the population vector as the statistics are expanded over the years of the population's life.

	Age 1+	Age 2+	Age 3+	Age 4+	Age 5+	Age 6+	Age 7+
Age 1+	0	0	0	0	0	0	0
Age 2+	0.696979	0	0	0	0	0	0
Age 3+	0	0.77958	0	0	0	0	0
Age 4+	0	0	0.2999918	0	0	0	0
Age 5+	0	0	0	0.2999918	0	0	0
Age 6+	0	0	0	0	0.2999918	0	0
Age 7+	0	0	0	0	0	0.2999918	0
Count Caught Rec	0	0	0.1046524	0.1046524	0.1046524	0.1046524	0
Count Caught Comm	0	0	0.1046524	0.1046524	0.1046524	0.1046524	0
Count Died Naturally	0.303021	0.22042	0.4907034	0.4907034	0.4907034	0.4907034	0
Weight Survived	0.01707599	0.03391173	0.02960919	0.03959892	0.04979865	0.06419825	0
Weight Caught Rec	0	0	0.01032919	0.01381411	0.0173723	0.02239561	0
Weight Caught Comm	0	0	0.01032919	0.01381411	0.0173723	0.02239561	0
Weight Died Naturally	7.424015m	9.588271m	0.04843242	0.06477285	0.08145676	0.1050105	0

Figure 6: Biomass Calculations Added into Leslie Transition Matrix

At Age 3, the probability coefficient for the biomass caught recreationally at Age 3 is equal to the probability of being caught recreationally at Age 3 (Rec. mortality rate) multiplied by the average weight at Age 3.

Probability Age3 caught recreationally	=	0.1046 (from Survival & Population section)	**(3.16)**
Weight at lifestage for an Age 3	=	0.0987 (from Yellow Perch mortality table)	**(3.17)**
Age 3 biomass coefficient for rec. catch	=	0.1046 * 0.0987 = 0.0103	**(3.18)**

When the population vector is multiplied by the transition matrix (Equation 3.1), the number of Age 3's will multiply by the biomass coefficient for weight caught recreationally under the Age 3 column. The result will represent the amount of biomass resulting from the recreational catch of Age 3's.

Figure 7 represents the expansion of a 2007 yellow perch population of 1,000 Age 1's, 50 Age 2's, and 10 Age 4's with the biomass components included in the population expansion.

	2007	2008	2009	2010	2011	2012	2013	2014
Age 1+	1000	0	0	0	0	0	0	0
Age 2+	50	696.979	0	0	0	0	0	0
Age 3+	0	38.979	543.3509	0	0	0	0	0
Age 4+	10	0	11.69338	163.0008	0	0	0	0
Age 5+	0	2.999918	0	3.507919	48.89892	0	0	0
Age 6+	0	0	0.899951	0	1.052347	14.66928	0	0
Age 7+	0	0	0	0.269978	0	0.3156955	4.400663	0
Count Caught Rec	0	1.046524	4.393194	58.18089	17.42554	5.227519	1.535175	0
Count Caught Comm	0	1.046524	4.393194	58.18089	17.42554	5.227519	1.535175	0
Count Died Naturally	0	318.949	174.2273	272.8037	81.70641	24.51126	7.198264	0
Weight Survived	0	19.16756	24.93929	16.609	6.629347	2.502659	0.9417419	0
Weight Caught Rec	0	0.1381411	0.454737	5.794063	2.312653	0.8730544	0.3285274	0
Weight Caught Comm	0	0.1381411	0.454737	5.794063	2.312653	0.8730544	0.3285274	0
Weight Died Naturally	0	8.551157	8.815035	27.16772	10.84377	4.093655	1.540428	0

Figure 7: Population Expanded with Biomass Components