

Diagnosics for multiyear tagging models with application to Atlantic striped bass (*Morone saxatilis*)

Robert J. Latour, John M. Hoenig, John E. Olney, and Kenneth H. Pollock

Abstract: Information on age- and year-specific survival can be obtained from multiyear tagging data using one of three classes of tag recovery models. Two of the model types yield information on total survival, while the third allows separation of total mortality into its fishing and “natural” components if information on the tag reporting rate is available. The performance of each class is usually assessed using goodness-of-fit tests, Akaike’s information criterion, and similar measures. However, we propose that examination of model residuals is also important for the evaluation of model performance and contend that at least four types of problems are potentially detectable via patterns in residuals. Those presented in this paper include nonmixing of newly tagged animals, emigration of older animals, cohort effects associated with initial tag-induced mortality or tag shedding, and a change in the natural mortality rate. We present the diagnostic procedures by analyzing a hypothetical tagging data set and discuss the various constraints inherent to the residuals of each class of models. The diagnostic procedures are also used to evaluate striped bass tagging (*Morone saxatilis*) data from the Hudson River and Chesapeake Bay.

Résumé : Trois classes de modèles de récupération d’étiquettes permettent d’obtenir de l’information sur la survie spécifique à l’âge ou à l’année à partir de données de marquage qui s’étendent sur plusieurs années. Deux des types de modèles renseignent sur la survie totale, alors que le troisième permet de séparer la mortalité due à la pêche des composantes « naturelles » de la mortalité, si l’on connaît le taux de signalisation des étiquettes. La performance de chaque classe de modèle est généralement mesurée par des tests d’ajustement, par le critère d’information d’Akaike et d’autres mesures similaires. Nous proposons que l’examen des résidus des modèles est important dans l’évaluation de leur performance et pensons qu’au moins quatre types de problèmes peuvent être détectés par l’étude de la structure des résidus. Les problèmes signalés ici comprennent, entre autres, la répartition non aléatoire des animaux nouvellement marqués dans la population, l’émigration des animaux plus âgés, les effets sur les cohortes de la mortalité associée au marquage ou à la perte des étiquettes et le changement du taux de mortalité naturelle. L’analyse d’une série de données de marquage hypothétiques illustre les méthodes diagnostiques; on y trouve aussi une discussion des diverses contraintes associées aux résidus de chaque classe de modèles. Les méthodes diagnostiques ont aussi servi à évaluer des données de marquage du Bar rayé (*Morone saxatilis*) du fleuve Hudson et de la baie de Chesapeake.

[Traduit par la Rédaction]

Introduction

The origin and development of multiyear tagging models that allow the estimation of age- and year-specific survival and tag recovery rates have been well documented. Early work by Seber (1970), Robson and Youngs (1971), and Youngs and Robson (1975) was generalized and presented in the context of migratory bird studies by Brownie et al. (1985). Although the Brownie models were originally applied mostly to waterfowl banding data, it has been noted

that the methodology can also be used to analyze fisheries tagging data. Pollock et al. (1991) and Hoenig et al. (1998a) showed that it is possible to convert tag recovery rates to fishing exploitation rates when information on the tag retention, tag-induced mortality, and tag reporting rate is available. They also demonstrated that it is possible to estimate instantaneous rates of fishing and natural mortality from fishing exploitation rates if additional information on the seasonal distribution of fishing intensity is known at least approximately. Hoenig et al. (1998b)

Received December 5, 2000. Accepted June 14, 2001. Published on the NRC Research Press Web site at <http://cjfas.nrc.ca> on August 9, 2001.
J16120

R.J. Latour,¹ J.M. Hoenig, and J.E. Olney. Department of Fisheries Science, Virginia Institute of Marine Science, College of William and Mary, Gloucester Point, VA 23062, U.S.A.

K.H. Pollock. Biomathematics Graduate Program, Department of Statistics, North Carolina State University, Raleigh, NC 27695, U.S.A.

¹Corresponding author (e-mail: latour@vims.edu).

extended the instantaneous rates formulation to allow for nonmixing of newly tagged animals among the general population.

Case studies that involve the application of Brownie-type models to fisheries data are numerous in recent years (Larson et al. 1991; Ross et al. 1995; Smith et al. 2000). However, in many respects, the rate of theoretical development of these models has greatly exceeded the rate at which tagging studies that adhere to their assumptions and design specifications are being conducted. In practice, application of the Brownie-type models generally requires that a large portion of the data analysis process involve investigation and evaluation of biases due to potential violation of assumptions. Violation of assumptions can sometimes be attributed to the species under study (e.g., rates of survival and tag recovery may not be homogeneous within years if some animals permanently emigrate from the study area) or to the design of the tagging study (e.g., nonmixing of newly and previously tagged animals may be problematic if tagging occurs in only a few locations).

The details associated with model building and model selection have always been widely recognized as important for good statistical inference. However, until recently, model selection has received little attention in most practical situations. In the realm of tagging models, two recent advances have precipitated changes in the model selection recommendations originally made by Brownie et al. (1985). Specifically, Burnham et al. (1995) advocated placing greater reliance on Akaike's information criterion (AIC) (Akaike 1973; Burnham and Anderson 1992) and other related measures such as quasi-likelihood AIC (QAIC) (Akaike 1985) over likelihood ratio tests; Buckland et al. (1997) and Burnham and Anderson (1998) suggested estimating survival as a weighted average from multiple models instead of searching for a single "best" model.

In this paper, we build on the themes of model building and model selection by proposing a series of diagnostic procedures that can be used in conjunction with goodness-of-fit (GOF), AIC, and QAIC measures to assess the performance of a model. In essence, we suggest that the fit of a model be evaluated by critically analyzing the model residuals and that distinct patterns in those residuals will be evident if particular assumptions are violated. We include two separate tagging data sets in our discussion of the various patterns. First, a hypothetical data set is used for the purposes of explanation and demonstration of the diagnostics. That example is then followed by an exploratory analysis of Atlantic striped bass (*Morone saxatilis*) tagging data from the Hudson River, New York, and both the Maryland and Virginia portions of Chesapeake Bay.

Review of multiyear tagging models and assumptions

Brownie et al. (1985), Model 1

Tag return data are generally represented by an upper triangular matrix of tag recoveries. For example, the matrix for a study with I years of tagging and J years of recovery would be

$$(1) \quad r = \begin{bmatrix} r_{11} & r_{12} & \dots & r_{1J} \\ - & r_{22} & \dots & r_{2J} \\ \vdots & \vdots & \ddots & \vdots \\ - & - & - & r_{IJ} \end{bmatrix}$$

where r_{ij} is the number of tags recovered in year j that were released in year i ($i = 1, \dots, I; j = 1, \dots, J; J \geq I$). Tagging periods do not necessarily have to be yearly intervals. However, data analysis is easiest if all periods are the same length and all tagging events are conducted at the beginning of each period. Application of the Brownie models involves constructing a matrix of expected values and comparing them with the observed data. The matrix of expected values corresponding to eq. 1 under Model 1 of the Brownie formulation would be

$$(2) \quad E(r) = \begin{bmatrix} N_1 f_1 & N_1 S_1 f_2 & \dots & N_1 S_1 \dots S_{J-1} f_J \\ - & N_2 f_2 & \dots & N_2 S_2 \dots S_{J-1} f_J \\ \vdots & \vdots & \ddots & \vdots \\ - & - & - & N_I f_I \end{bmatrix}$$

where N_i is the number tagged in year i , f_i is the tag recovery rate in year i , and S_i is the survival rate in year i . Since the data in each row of the matrix follow a multinomial distribution, the method of maximum likelihood can be used to derive parameter estimates. Also, since all tagged cohorts are assumed to be independent, the overall likelihood function is simply the product of the individual likelihood functions corresponding to each row of the recovery matrix (Brownie et al. 1985; Hoenig et al. 1998a). Software packages that numerically maximize the multinomial likelihood function have been developed for application of the Brownie and other tagging models. These include programs SURVIV (White 1983) and MARK (White and Burnham 1999).

Seber (1970), Model 1*

Seber (1970) proposed a class of tag recovery models very similar to those described by Brownie et al. (1985). The only difference lies in the definition of the tag recovery rate. Specifically, Seber (1970) modeled the tag recovery rate as $f = (1 - S)r$, where r is the rate at which tags are reported from killed fish regardless of the source of mortality. Application of the time-specific parameterization of the Seber (1970) models, which we will refer to as Model 1*, again involves comparing a matrix of expected values with observed data. Program MARK can be used to numerically maximize the product likelihood function and ultimately obtain parameter estimates for this class of models.

Hoenig et al. (1998a), the instantaneous rates (IR) models

Hoenig et al. (1998a) reparameterized the Brownie models in terms of instantaneous rates of fishing mortality (F) and natural mortality (M) and showed how information on fishing effort could be used to partition total mortality into its fishing and natural components. Application of the IR models also involves constructing a matrix of expected recoveries. Under the formulation of a model that specifies time-specific fishing mortality rates and a constant natural

mortality rate, the matrix of expected values corresponding to eq. 1 would be

$$(3) \quad E(r) = \begin{bmatrix} N_1 \phi \lambda u_1(F_1, M) & N_1 \phi \lambda u_2(F_2, M) e^{-(F_1+M)} & \dots & N_1 \phi \lambda u_J(F_J, M) e^{-\left(\sum_{k=1}^{J-1} F_k + (J-1)M\right)} \\ - & N_2 \phi \lambda u_2(F_2, M) & \dots & N_2 \phi \lambda u_J(F_J, M) e^{-\left(\sum_{k=2}^{J-1} F_k + (J-2)M\right)} \\ \vdots & \vdots & \ddots & \vdots \\ - & - & - & N_I \phi \lambda u_J(F_J, M) \end{bmatrix}$$

where ϕ is the short-term probability of surviving the tagging process with the tag intact, λ is the tag reporting rate (ϕ and λ are considered constant over time), and $u_k(F_k, M)$ is the exploitation rate in year k (u_k is a function of F_k and M and depends on the seasonal pattern of fishing). When fishing occurs continuously throughout the year with constant intensity, the exploitation rate is (Ricker 1975)

$$u_k(F_k, M) = \frac{F_k}{F_k + M} (1 - e^{-F_k - M})$$

Again, the recapture data follow the multinomial distribution and parameter estimates are obtained by maximizing an overall product multinomial likelihood function. An S-PLUS-based program entitled AVOCADO (J.M. Hoenig et al., unpublished data) has been developed to fit this class of models.

Assumptions of multiyear tagging models

Application of the Brownie models requires making the following assumptions (see Pollock et al. (1991, 2001) for critical reviews of these assumptions as they relate to the analysis of fisheries tagging data): (1) the tagged sample is representative of the target population, (2) there is no tag loss, (3) survival rates are not affected by tagging, (4) the year of tag recovery is correctly reported, (5) the fate of each tagged fish is independent, and (6) all tagged fish within a cohort are subject to the same annual survival rate and recovery rate. Since development of the IR formulation was based on the traditional Brownie models, it follows that application of these models requires making those assumptions outlined above. However, two additional assumptions are also required: (7) fishing and natural mortality processes are additive and (8) the tag reporting rate is known. In theory, the tag reporting rate can be estimated from the tagging data if it is constant over time. However, Hoenig et al. (1998a) found that massive numbers of recaptures are necessary to get reliable estimates. Hence, external information about the tag reporting rate is often needed (e.g., from a high-reward tagging study or catch sampling program).

Residuals of Model 1 and Model 1*

Because the diagnostic procedures that we propose involve searching for patterns in the residuals, it is necessary to briefly discuss the structure of the residuals associated with Model 1 and Model 1*. A critical analysis revealed that several of the residuals associated with these models are always zero. Specifically, the relationship $E(r_{11}) = r_{11}$ always holds, regardless of the number of years of tagging and recovery. That is, the observed data and the expected value as-

sociated with the (1,1) cell are always identical, which implies that the residual for that cell is always equal to zero. Further, it can be shown that the residuals associated with the implicit “never seen again” category are also always equal to zero (analytical proof of these properties is available from R.J. Latour). Given these characteristics, the matrix of residuals derived from analyzing tag recovery data for a study with I years of tagging and J years of recovery under Model 1 or Model 1* takes the form

$$\text{resid} = \begin{bmatrix} 0.00 & (r_{12} - E_{12}) & \dots & (r_{1J} - E_{1J}) & 0.00 \\ - & (r_{22} - E_{22}) & \dots & (r_{2J} - E_{2J}) & 0.00 \\ \vdots & \vdots & \ddots & \vdots & 0.00 \\ - & - & \dots & (r_{IJ} - E_{IJ}) & 0.00 \end{bmatrix}$$

where r_{ij} is the observed number of tag recoveries and E_{ij} is the corresponding expected number of tag recoveries (the above matrix has $J + 1$ columns because a column has been added on the right to account for fish that were tagged and never recaptured). It is also true that the sum of each row and each column of the residuals matrix must equal zero. For the case when $I = J$ (i.e., the recovery matrix is square), an additional constraint that $E(r_{II}) = r_{II}$ is present. Which implies that the residual for the (I,I) cell is always equal to zero.

When searching for patterns in the residuals, the fact that those values associated with the (1,1) and the “never seen again” cells are zero essentially implies that fewer residual values are available for inspection. For example, examination of row 1 for a pattern will involve only $J - 1$ residuals rather than the $J + 1$ that are inherent to the model. Similarly, when $I = J$ and the recovery matrix is square, the J th column only contains $J - 1$ residuals that can be scrutinized for a pattern. Having fewer available residuals is not overly problematic; rather, it just implies that conclusions about the existence of patterns may be based on fewer values. With the exception of the row sums having to be zero, the residuals given by program AVOCADO for all parameterizations of the IR models are not subject to the aforementioned constraints.

Diagnostic procedures

When fitting a multiyear tagging model, it is important to determine if any of the underlying assumptions have been violated. If model assumptions are not supported by the data, then it is likely that parameter estimates obtained from the analysis will be unreliable. One approach for evaluating model fit involves comparing the observed and expected

Table 1. Hypothetical perfect data generated by arbitrarily choosing $S_1 = 0.66$, $S_2 = 0.70$, $S_3 = 0.67$, $S_4 = 0.63$, $f_1 = 0.11$, $f_2 = 0.09$, $f_3 = 0.10$, $f_4 = 0.13$, and $f_5 = 0.11$ under Model 1 or, alternatively, $F_1 = 0.27$, $F_2 = 0.21$, $F_3 = 0.25$, $F_4 = 0.32$, $F_5 = 0.26$, $M = 0.15$, and $\phi\lambda = 0.50$ under the IR formulation with continuous fishing throughout the year.

Year	Number tagged	Number recaptured in year				
		1	2	3	4	5
1	1100	121	64	52	43	23
2	950		84	68	57	30
3	845			87	72	38
4	1020				130	68
5	990					106

Note: The recoveries were rounded to the nearest whole number. Consequently, the residuals from fits of Model 1 and an IR model are not exactly zero, but the largest residual in absolute value was less than 0.40.

numbers of tag recoveries. This comparison constitutes the basis for the formal GOF test, which is used to test the null hypothesis that the model fits the data. Although the GOF test is informative, rejection of the null hypothesis does not provide any information about why the model does not fit the data or which assumption(s) is (are) possibly in violation. Also, failure to reject the null hypothesis of a good fit does not necessarily imply that all assumptions are met. We propose a more systematic approach for assessing model performance and suggest that certain patterns in model residuals can be indicative of particular assumption violations.

Example 1. Explanation of diagnostics using a hypothetical perfect data set

For the purposes of explanation and demonstration, a hypothetical perfect data set (i.e., the observed number of tag recoveries is equal to the expected number of tag recoveries) that reflects 5 years of tagging and recovery was created (Table 1). The expected values were generated under Model 1 with arbitrarily chosen parameter values $S_1 = 0.66$, $S_2 = 0.70$, $S_3 = 0.67$, $S_4 = 0.63$, $f_1 = 0.11$, $f_2 = 0.09$, $f_3 = 0.10$, $f_4 = 0.13$, and $f_5 = 0.11$. The data in Table 1 can also be generated under the IR formulation with parameter values $F_1 = 0.27$, $F_2 = 0.21$, $F_3 = 0.25$, $F_4 = 0.32$, $F_5 = 0.26$, $M = 0.15$, and the product $\phi\lambda = 0.50$ assuming that fishing is continuous throughout the year.

To demonstrate the patterns in model residuals that develop when particular assumptions are violated, the true recovery matrix was modified to simulate five specific scenarios: nonmixing, emigration from the study area (a form of heterogeneity), tag-induced mortality, a change in the natural mortality rate, and a change in the tag reporting rate (note that this is only an assumption violation of the IR model). Since analysis of the unmodified data produces residuals exactly equal to zero, fitting a model to each of these modified data sets explicitly reveals the patterns in residuals that arise when a particular assumption is violated. When applicable, Model 1, Model 1*, and a time-specific IR model (assuming the product $\phi\lambda = 0.50$) were fit to the data using programs MARK and AVOCADO. In all cases, the patterns evident in the residuals of Model 1 were also expressed in those of Model 1*. Hence, we only refer to the residuals of Model 1 and the IR model in the discussion that follows. Also, we do

not discuss in detail the change in tag reporting rate scenario, since it was not possible to detect violation of this assumption via a pattern in the residuals of the IR model.

Nonmixing

This constitutes violation of assumption 1, where newly tagged fish are not thoroughly mixed with previously tagged fish. Nonmixing of newly tagged fish among cohorts can result from a lack of dispersal (i.e., clustering) immediately after tagging. It may be that the natural migratory behavior of the species under study is such that dispersal and mixing of a released cohort of tagged fish requires more time than that defined by the tagging period of the analysis.

In their discussion of nonmixing, Hoenig et al. (1998b) intentionally modified the lake trout tagging data from Cayuga Lake, New York (Youngs and Robson 1975), to simulate a nonmixing scenario. A similar approach was adopted here to create a nonmixing situation with the recovery data in Table 1. Specifically, the number of recaptures along the main diagonal were multiplied by two thirds to simulate a situation where the exploitation rate of newly tagged fish is two thirds that of previously tagged fish (Table 2a). Since the survival rate in the year of tagging is higher, the number of recaptures in subsequent years had to be adjusted upwards. To do so, the natural mortality rate and fishing mortality rates associated with the original data were used to calculate a cohort-specific exploitation rate for each year of tagging. New fishing mortality rates, F_i^* , that reduced the exploitation rates to two thirds of their original value were identified through an iterative process. For each row of the recovery matrix, all entries to the right of the main diagonal were then multiplied by the ratio of survival rates (i.e., $\exp(F_i - F_i^*)$, where F_i is the original fishing mortality rate).

The fit of both Model 1 and the IR model to the data in Table 2a is extremely poor, as evident from the results of the GOF test (Model 1: $\chi^2_{6df} = 18.23$, $p < 0.006$; IR model: $\chi^2_{9df} = 20.2$, $p < 0.02$). However, an alternative indication that both models fit poorly is given by the consistently negative residuals on the main diagonal and positive residuals on the super diagonal of the residuals matrix for each model (Table 2b). It is clear that the residuals from both models possess the pattern; however, the restrictions that the (1,1) and (I,I) residuals of Model 1 are always zero forces the determination of the pattern to be based on fewer cells. Since the residuals of the IR model do not possess those same constraints, the negative pattern on the main diagonal is more obvious.

If newly tagged fish tend to remain clustered after they are released, the distribution of those individuals will be different from that of those that were tagged on prior sampling occasions. Suppose tagged fish are released in areas that are not prime fishing locations. Then newly tagged fish will be less available to fishers. A model that assumes that all tagged cohorts are well mixed cannot account for the reduced availability of newly tagged fish. Hence, the number of observed tag recoveries will be consistently smaller than the expected number of tag recoveries in the year of tagging, and a pattern of negative residuals will emerge on the main diagonal. Since nonmixing in this case causes the survival rate in the year of tagging to be abnormally high, there will be more tagged fish available for harvest in later years. A

Table 2. Tagging data from Table 1 modified to simulate incomplete mixing in the year of tagging, and residuals from fitting Model 1 and an IR model (residuals for the IR model in parentheses).

(a) Hypothetical data modified to simulate nonmixing in the year of tagging ^a						
Year	Number tagged	Number recaptured in year				
		1	2	3	4	5
1	1100	81	70	57	48	25
2	950		56	74	61	32
3	845			58	79	41
4	1020				87	77
5	990					70

(b) Model residuals from fitting Model 1 and an IR model						
Number recaptured in year						
1	2	3	4	5	Never seen	
0.00 (-0.62)	10.43 (9.25)	1.13 (-0.74)	-3.67 (-5.79)	-7.88 (-7.94)	0.00 (5.83)	
	-10.43 (-9.65)	11.70 (11.60)	3.39 (2.87)	-4.66 (-3.60)	0.00 (-1.22)	
		-12.83 (-10.60)	13.50 (15.09)	-0.68 (1.86)	0.00 (-6.35)	
			-13.22 (-11.21)	13.22 (16.86)	0.00(-5.66)	
				0.00 (-7.17)	0.00 (7.17)	

^aExploitation of newly tagged fish was assumed to be two thirds that of previously tagged fish (see text for a full description of the modified data).

model that assumes complete mixing among tagged cohorts cannot adjust for an increase in availability of tagged fish in later years. Hence, the expected number of tag recoveries on the super diagonal will be abnormally low and consistently positive residuals will emerge (note that if newly tagged animals are released in areas that are intensely fished, the opposite pattern will appear with the main diagonal having positive residuals).

Hoenig et al. (1998b) showed that the presence of nonmixing can lead to seriously biased parameter estimates if a model that assumes that all tagged cohorts are well mixed is used for data analysis. Further, they demonstrated how to model nonmixing explicitly using the IR formulation and pointed out that the Brownie models cannot be parameterized to account for this potential problem. The detection of nonmixing is certainly not trivial. Data inspection cannot be used, and it is not always possible to determine if the study design itself will facilitate proper dispersal of tagged fish (see Bertignac et al. (1999) for an example of how the availability of the tagged population changes over time). To assist with this problem, Latour et al. (2001b) developed a simple test for nonmixing that can be applied prior to any data analysis if tag recovery locations are known.

Emigration

This constitutes violation of assumption 6 where survival or rate of disappearance among tagged fish within a cohort is variable in a particular year. This can occur if, for example, a tagged cohort comprises several age groups and older tagged fish commence a migratory pattern that causes them to permanently leave the study area. This can also occur if the various age groups of fish within a tagged cohort exhibit different rates of chronic tag loss due to tag fouling and (or) degradation (see Henderson-Arzapalo et al. (1999) for a discussion of tag degradation) or suffer an increase in mortality due to senility.

Emigration was introduced into the recovery data in Table 1 by postulating that any changes in mortality due to

movement only occur after a cohort of tagged fish has been at liberty at least 2 complete years. To simulate a scenario in which emigration increases over time, the number of recaptures in recovery years 3, 4, and 5 was reduced by 20, 30, and 40%, respectively, for the cohorts that were affected (Table 3a). Essentially, manipulation of the recovery data involved adjusting the number of recaptures along diagonals in the upper right corner of the matrix. Hence, the recoveries associated with cohorts 4 and 5 were unchanged in this scenario.

Unlike the nonmixing scenario, the GOF tests associated with both models suggest that the model fit is adequate (Model 1: $\chi^2_{6df} = 2.15$, $p < 0.91$; IR model: $\chi^2_{9df} = 2.35$, $p < 1.00$). However, definitive patterns in the residuals from both models are apparent. In particular, the residuals corresponding to the diagonals in the upper right corner of the matrix (excluding the "never seen again" column) are predominantly negative (Table 3b). Since the oldest tagged fish are generally those that are tagged at the beginning of the study and recaptured near the end of the study, it follows that there would be fewer recaptures along the diagonals in the upper right corner of the matrix if age-related emigration from the study area is evident. Consistently fewer observed than expected recoveries in that particular corner of the matrix will clearly cause the residuals to be negative. It should also be noted that the patterns discovered with the nonmixing scenario are also present in Table 3. Although this suggests that violation of assumptions 1 and 6 may be indistinguishable, the presence of negative residuals on both the main diagonal and the upper right corner of the residuals matrix is indicative of a problem that the GOF test was unable to detect. In this situation, questions should be asked about the study design (e.g., is tagging occurring in a few proximal locations or many disparate locations) and the life history of the species (e.g., at some point, will the species take on a migratory pattern that causes it to leave the study area) to identify the nature of the problem.

To account for possible senescence and emigration, a re-

Table 3. Tagging data from Table 1 modified to simulate emigration/senescence after years at liberty, and residuals from fitting Model 1 and an IR model (residuals for the IR model in parentheses).

(a) Hypothetical data modified to simulate emigration/senescence of older animals ^a						
Year	Number tagged	Number recaptured in year				
		1	2	3	4	5
1	1100	121	64	47	35	16
2	950		84	68	51	24
3	845			87	72	34
4	1020				130	68
5	990					106

(b) Model residuals from fitting Model 1 and an IR model						
Number recaptured in year						
1	2	3	4	5	Never seen	
0.00 (-0.18)	3.67 (3.56)	1.19 (-1.55)	-1.40 (-1.82)	-1.08 (-1.02)	0.00 (1.00)	
	-3.67 (-3.89)	5.22 (4.67)	-0.64 (-1.26)	-0.92 (-0.84)	0.00 (1.31)	
		-4.03 (-3.15)	5.81 (6.14)	-1.78 (-1.08)	0.00 (-1.92)	
			-3.77 (-2.48)	3.77(5.47)	0.00(-2.98)	
				0.00 (-2.49)	0.00 (2.49)	

^aThe number of recaptures in recovery years 3–5 was reduced by 20, 30, and 40% for animals at large for 3, 4, and 5 years, respectively.

cent innovation known as the “chop” option has been developed (Latour et al. 2001a). Essentially, the data in the upper right corner of the recovery matrix are ignored by adding those recaptures to the “never seen again” column. This will correct for some bias due to violation of assumption 6; however, subsequent parameter estimates may be less precise, since estimation is based on fewer overall data.

Tag-induced mortality

This constitutes violation of assumption 3 and an element of assumption 2, where the survival of a particular cohort of tagged fish is substantially reduced by the tagging process or tags are lost shortly after tagging. This can occur if the tagging crew changes and new members do not have much experience handling or tagging fish.

To simulate the effects of tag-induced mortality or immediate loss of tags due to tagging inexperience in year 2, the recaptures in Table 1 corresponding to cohort 2 were reduced by 20% in each recovery year (Table 4a). As with the emigration scenario, data analysis yielded GOF test statistics that were quite small (Model 1: $\chi^2_{6df} = 0.34, p < 1.00$; IR model: $\chi^2_{9df} = 2.28, p < 1.00$), which implies that both models fit the data well.

Because simulation of tag-induced mortality involved reducing the number of recaptures associated with cohort 2, it is reasonable to speculate that the effects of excessive tag-induced mortality would cause the residuals corresponding to the recaptures of cohort 2 to all be negative in both models. Although this is the case with row 2 of the IR residuals matrix, the same was not found with that of Model 1 (Table 4b). Since the residuals corresponding to the “never seen again” cells of Model 1 are always zero, and since each row sum of the residuals matrix must total zero, Model 1 cannot express a row pattern. Hence, from a diagnostics perspective, the constraints associated with the residuals of Model 1 render it very difficult to detect assumption violations that are cohort specific.

The residuals of the IR model are much more informative than those of Model 1 for the detection of assumption violations that are cohort specific. As with the residuals of Model 1, the row sums of the IR residuals matrix must also total zero. However, since the residuals associated with the “never seen again” cells of the IR model can assume positive or negative values, the expression of distinct row patterns is possible. This freedom makes it possible for the residuals of the recovery-year cells specific to a single cohort to all take on values of the same sign (i.e., the “never seen again” residuals can adjust for the row patterns). This is evident in Table 4b, since rows 1, 3, and 4 all possess positive recovery-year residuals and, as expected under the current scenario, row 2 possesses all negative residuals (row 5 is uninformative since it contains only one residual corresponding to a recovery year).

A change in the natural mortality rate

In theory, the class of models developed by Hoenig et al. (1998a) can be parameterized in terms of year-specific fishing and natural mortality rates. However, the desire for a parsimonious model often creates a need to assume that *M* is constant over time and over recruited ages in fisheries assessments. In spite of this, it is certainly possible for *M* to vary over time, since extreme seasonal temperatures, limitation of nutrients, and (or) pollution effects could all cause *M* to increase in a particular year.

To simulate the effects of a variable *M*, the recaptures in recovery year 5 of Table 1 were adjusted to reflect an *M* value of 0.45 (Table 5a). Even though the GOF test suggests that the fit of the IR model with a constant *M* is adequate ($\chi^2_{9df} = 12.2, p < 0.20$), a distinct pattern of negative residuals is present in column 5 of the residuals matrix (Table 5b). The increase in *M* caused the number of recaptures in column 5 of Table 1 to decrease. This is not surprising, since a higher *M* essentially implies that fewer tagged fish will be available to fishers. By assuming that *M* is constant over time, the IR

Table 4. Tagging data from Table 1 modified to simulate tag-induced mortality/tag loss, and residuals from fitting Model 1 and an IR model (residuals for the IR model in parentheses).(a) Hypothetical data modified to simulate tag-induced mortality/tag loss endured by cohort 2^a

Year	Number tagged	Number recaptured in year				
		1	2	3	4	5
1	1100	121	64	52	43	23
2	950		67	55	45	24
3	845			87	72	38
4	1020				130	68
5	990					106

(b) Model residuals from fitting Model 1 and an IR model

Number recaptured in year						Never seen
1	2	3	4	5		
0.00 (3.35)	0.08 (7.43)	-0.08 (4.23)	-0.14 (2.99)	0.24 (1.93)	0.00 (-19.92)	0.00 (31.48)
	-0.08 (-9.08)	0.24 (-9.25)	-0.27 (-8.81)	0.12 (-4.34)	0.00 (-8.54)	0.00 (-4.18)
		-0.06 (4.29)	0.03 (2.72)	0.03 (1.52)	0.00 (-0.30)	0.00 (0.30)
			0.38 (3.04)	-0.39 (1.14)		
				0.00 (-0.30)		

^aThe number of recaptures corresponding to cohort 2 in recovery years 2–5 was each reduced by 20%.**Table 5.** Tagging data from Table 1 modified to simulate a change in the natural mortality rate M , and residuals from fitting an IR model that assumes that M is constant.(a) Hypothetical data modified to simulate a change in M^a

Year	Number tagged	Number recaptured in year				
		1	2	3	4	5
1	1100	121	64	52	43	6
2	950		84	68	57	11
3	845			87	72	18
4	1020				130	44
5	990					92

(b) Model residuals from fitting Model 1 and an IR model

Number recaptured in year						Never seen
1	2	3	4	5		
2.02	3.43	4.86	6.41	-5.16	-11.56	-11.56
	-2.05	1.03	5.01	-4.85	0.87	0.87
		-6.24	-0.38	-4.07	10.68	10.68
			-14.64	-0.10	14.74	14.74
				13.98	-13.98	-13.98

^aThe value of M was increased from 0.15 to 0.45 in year 5.

model cannot account for the systematically fewer recaptures in recovery year 5, and the residuals associated with that recovery year are consistently negative (in cases where M decreased in a particular year, a column pattern of positive residuals would emerge). It should be noted that the change in M precipitated the development of row patterns. Specifically, the residuals in row 1 are consistently positive and the residuals in rows 3 and 4 are strictly negative.

Subtle changes in M do not readily create column patterns in the matrix of residuals. Simulations where M was only slightly changed in a particular year failed to produce consistent patterns of negative or positive residuals. Since the detection of a change in M is not trivial, we suggest that

year-specific auxiliary data (e.g., prey indices, water temperature, etc.) be used in combination with examination of residuals to determine the likelihood of a change in M .

Sensitivity of diagnostics under the IR formulation

Because the partition of total mortality into its fishing and natural components is sensitive to the estimate of $\phi\lambda$ (Latour et al. 2001a), we varied the value of $\phi\lambda$ to determine if the aforementioned patterns in residuals were apparent under conditions when the true and assumed values of $\phi\lambda$ were substantially different. Since the hypothetical data were generated with a value of 0.50 for $\phi\lambda$, we reanalyzed the data associated with the nonmixing, emigration, tag-induced mor-

Table 6. Tag recovery data for striped bass >711 mm total length that were tagged in the Rappahannock River, Virginia, and residuals from fitting Model 1*.

<i>(a)</i> Release and recovery data for striped bass in the Rappahannock River, Virginia													
Year	Number tagged	Number recaptured in year											
		1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999
1988	56	7	7	4	1	0	2	0	0	0	1	0	0
1989	101		4	4	3	3	0	2	0	0	0	1	0
1990	300			26	9	15	2	3	7	1	0	2	1
1991	390				41	24	16	11	3	2	2	1	2
1992	40					4	3	2	2	0	0	0	1
1993	212						22	18	7	5	6	0	0
1994	123							9	7	5	1	2	0
1995	209								28	10	8	3	3
1996	66									1	3	1	0
1997	212										15	13	8
1998	158											24	13
1999	162												16

<i>(b)</i> Residuals from fitting Model 1*												
Number recaptured in year												
1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	Never seen
0.00	3.41	1.32	-0.46	0.00	1.42	0.00	0.00	0.00	0.91	0.00	0.00	-4.55
	-3.41	-1.53	0.00	0.72	0.00	1.08	0.00	0.00	0.00	0.88	0.00	4.55
		0.21	-5.01	4.33	-3.59	-1.30	4.16	-0.09	0.00	1.45	0.67	0.00
			5.47	-3.06	1.81	0.09	-4.16	-0.75	-0.12	-0.41	1.17	0.00
				-0.89	0.44	0.03	0.70	0.00	0.00	0.00	0.85	0.00
					1.12	1.93	-3.59	0.947	2.88	0.00	0.00	0.00
						-1.39	0.15	2.38	-1.02	0.66	0.00	0.00
							3.66	0.69	0.83	-1.77	0.19	-3.60
								-2.33	0.44	-0.70	0.00	3.60
									-2.51	1.37	1.15	0.00
										0.92	-0.59	-0.32
											-0.32	0.32

tality, and variable *M* scenarios using values of $\phi\lambda$ that ranged from 0.30 to 0.80.

For all values of $\phi\lambda$ considered, the patterns in residuals associated with each scenario remained evident. In fact, for the nonmixing and emigration cases, a cell-by-cell comparison of the matrices of residuals showed that the signs of all residuals remained unchanged. The same cell-by-cell preservation of positive and negative residuals was predominately evident when the tag-induced mortality and variable *M* residuals matrices were compared. For the tag-induced mortality scenario, the only differences were with row 5 of the $\phi\lambda = 0.60, 0.70,$ and 0.80 scenarios. In all three instances, the residual associated with recovery year 5 was negative and the corresponding “never seen again” residual was positive (the exact opposite pattern is present in row 5 of the $\phi\lambda = 0.50$ residuals matrix). For the variable *M* scenario, the only differences were when $\phi\lambda = 0.30$ and 0.40 , since three of the five residuals in column 5 were negative instead of four out of five.

Example 2. Exploration of Atlantic striped bass tagging data

The Atlantic striped bass has historically supported several important recreational and commercial fisheries along the eastern coastline. During the 1960s and 1970s, overfish-

ing, pollution, and reduction of spawning habitat precipitated steady declines in the abundance of virtually all stocks in the Atlantic. In response to the documented decline, the Atlantic States Marine Fisheries Commission sponsored the development of an interstate fisheries management plan that took effect during the mid-1980s. The fisheries management plan called for the establishment of a cooperative tagging program (which currently involves 15 state and federal agencies) so that information on migration, relative contribution to the coastal population, and annual survival of Atlantic striped bass stocks could be evaluated. At present, the agencies participating in the cooperative tagging program continue to tag thousands of striped bass each year.

The current protocol to analyze the tagging data, as established by the Atlantic States Marine Fisheries Commission Striped Bass Technical Committee, involves deriving survival estimates from a suite of Seber (1970) models. Tag recoveries from striped bass that were >711 mm total length at the time of tagging are analyzed because they constitute the migratory population and are believed to be fully recruited to the coastal fishery. The analysis consists of four steps. First, a set of biologically reasonable candidate models is identified prior to the data analysis. These models are then fit to the tagging data, and AIC and GOF diagnostics are used to evaluate their fit (Burnham et al. 1995). The overall

Table 7. Residuals from fitting Model 1* to striped bass tagging data from the Maryland portion of Chesapeake Bay (1988–1997), and residuals from fitting Model 1* to striped bass tagging data from the Hudson River, New York (1988–1997).

(a) Residuals from fitting Model 1* to the Maryland striped bass tagging data										
Number recaptured in year										
1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	Never seen
0.00	3.17	-1.08	5.97	0.35	-0.29	0.53	0.00	0.00	0.00	-6.12
	-3.17	0.84	1.71	-0.49	-0.07	0.39	2.65	0.73	0.00	-1.76
		0.24	-6.00	0.46	-0.99	-1.84	0.55	0.00	1.65	7.79
			-1.68	-1.11	5.13	-2.90	0.01	-1.32	1.88	0.00
				0.78	-0.61	-2.80	-0.17	0.33	2.46	0.00
					-3.17	5.45	2.62	-6.69	1.79	0.00
						1.17	-1.02	0.26	-0.41	0.00
							-3.32	0.15	3.17	0.00
								9.11	-9.11	0.00
									0.00	0.00

(b) Residuals from fitting Model 1* to the Hudson River striped bass tagging data										
Number recaptured in year										
1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	Never seen
0.00	1.52	-1.30	1.79	2.39	0.09	2.42	0.00	1.63	1.02	-7.68
	-1.52	-1.02	-0.59	-4.63	-0.52	2.06	2.12	0.00	0.00	7.68
		2.32	-0.51	4.25	0.31	-2.70	-0.64	-3.11	0.08	0.00
			-0.69	0.15	-3.63	1.23	1.85	1.79	-0.70	0.00
				-2.16	1.07	0.16	-0.84	-1.92	3.70	0.00
					2.68	1.20	-6.21	-0.11	2.44	0.00
						-4.38	-1.22	1.79	3.81	0.00
							6.82	-3.40	-3.42	0.00
								5.43	-5.43	0.00
									0.00	0.00

estimates of survival are then calculated as a weighted average of survival from the best-fitting models, where the weight is related to the AIC value (i.e., the better the AIC, the higher the weight) (Buckland et al. 1997; Burnham and Anderson 1998; Smith et al. 2000).

We examined the residuals associated with the application of Model 1* to striped bass tagging data from the Hudson River, New York, the Maryland portion of Chesapeake Bay (see Smith et al. (2000) for the data from those regions) and the Rappahannock River, Virginia (Table 6a), to determine if model assumptions were in violation. In each of the three residuals matrices, the symptoms associated with a nonmixing or emigration problem were not present (Tables 6b and 7). The lack of nonmixing with the Rappahannock River data is consistent with the findings of Latour et al. (2001b), who performed a spatial analysis of the tag recoveries. Given the migratory behavior of striped bass >711 mm total length, this result is not surprising and it seems likely that a similar spatial analysis of the New York and Maryland data would also show that lack of mixing is not problematic. Emigration should also not be problematic, since the recovery areas for all three analyses encompass the entire eastern seaboard.

Inspection of the “never seen again” columns of the three residuals matrices does suggest that there are cohort-specific problems with the application of Model 1*. For the Virginia data, the residuals associated with the “never seen again” category of rows 1, 2, 8, 9, 11, and 12 were nonzero (Table 6b). A more detailed examination of the recovery data for the cohorts tagged in 1988 and 1989 showed that in 1989, there were approximately twice as many fish tagged as

in 1988, but comparatively, only about half the number of tag recoveries were observed each year from the 1989 cohort. Since the data in rows 1 and 2 of the recovery matrix are needed for the estimation of S_1 , it seemed likely that the problem would also be apparent with the estimate of S_1 . Although there was nothing unusual about the estimate of S_1 from Model 1* ($S_1 = 0.88$), application of Model 1 (via program MARK) to the data in Table 6a yielded an estimate of exactly 1.00 for S_1 . This estimate resulted because the program was forced to impose the constraint that all survival estimates must be between 0.00 and 1.00 during the estimation process.

Hand calculation of the estimate for S_1 under Model 1 from the analytical formula of the maximum likelihood estimate given by Brownie et al. (1985) yielded a value of 1.59 for S_1 . (If the identity link in program MARK is used with Model 1, then hand calculations are not needed because MARK will provide the appropriate maximum likelihood estimates and residuals for situations where inadmissible survival estimates arise. However, the identity link does not work with Model 1* because the term $(1 - S)$ appears directly in the likelihood, and negative probability values are generated when inadmissible survival estimates arise.) Clearly, a survival probability cannot exceed 1.00, and the fact that the data yield an inadmissible value under Model 1 suggests that there is a problem with the 1989 cohort. Since a hand calculation of S_8 yielded an estimate of 1.68, it appears that there is also a problem with the 1996 cohort. However, in 1996, only 66 fish were tagged, and only a total of five recoveries were tabulated over the 4 years that the co-

hort was at liberty. Hence, the noted problem with S_8 and the 1996 cohort may be a result of sparse data. It is unclear why the “never seen again” residuals in rows 11 and 12 are nonzero, since hand calculation of S_{11} yielded a value of 0.89. Perhaps the constraints imposed for the estimation of S_1 and S_8 caused problems with the estimation of other parameters (it is unclear how the estimation process is affected when boundary values are reached).

For the Maryland data, the residuals associated with the “never seen again” category of rows 1–3 were nonzero (Table 7a). The estimates of S_1 and S_2 from Model 1* were high ($S_1 = 0.96$ and $S_2 = 0.94$), but given the fact that striped bass in Maryland were under moratorium until 1990, high rates of survival for 1988 and 1989 should be expected. However, application of Model 1 yielded estimates of exactly 1.00 for S_1 and S_2 and hand calculations of S_1 and S_2 yielded values of 1.10 and 1.11, respectively. These results are nonsensical and they suggest that there may be problems with the 1989 and 1990 cohorts. This same trend was also apparent with the New York data, since the “never seen again” residuals associated with rows 1 and 2 were nonzero (Table 7b). Again, the estimate of S_1 from Model 1* was high ($S_1 = 0.90$), but the hand calculated value under Model 1 was 1.06, which again suggests that there may be a problem with the 1989 cohort.

Examination of the residuals matrices (not shown here) associated with application of an IR model to each of the recovery matrices confirmed the noted cohort-specific problems. For the Virginia data, rows 2 and 8 of its residuals matrix revealed negative residuals for eight out of 11 and four out of four values, respectively. For the New York data, nine out of 10 residuals in row 1 were positive, while seven out of nine residuals were negative in row 2. For the Maryland data, row 3 of the residuals matrix showed a distinct pattern, since seven out of eight values were negative. Patterns in rows 1 and 2 were slightly less apparent, since seven out of 10 and five out of nine residuals were positive, respectively.

Discussion

We have shown that specific patterns in the residuals of multiyear tagging models arise when particular assumptions are violated. In particular, patterns along the main and super diagonals are evident when nonmixing is problematic, and patterns of consistently negative residuals are present in the upper right corner of the residuals matrix when the survival or rate of disappearance among tagged fish within a cohort is variable because of emigration. Although the patterns in residuals associated with emigration seem to be indistinguishable from those of nonmixing, the two phenomena are generally separable if the sampling design and the life history of the species under study are critically examined to determine which is more likely to be evident in the study. The presence of distinctive row patterns in the residuals matrix is indicative of short-term tag-induced/handling mortality and tag loss. A change in the natural mortality rate can cause a column effect of the IR model residuals.

An inspection of the residuals matrix for patterns should accompany the more traditional measures of model fit (e.g., AIC and GOF) as fundamental parts of evaluating the performance of multiyear tagging models. In addition to consid-

ering multiple model parameterizations, the analysis of tagging data should also involve all available model types (i.e., Brownie et al. (1985) and Hoenig et al. (1998a, 1998b) models) regardless of the goal of the study or the desired parameters estimates. Application of a suite of model types to tagging data increases the amount of information that can be used for the evaluation of assumption violation. The value of this approach is particularly exemplified by the fact that the residuals of the IR models do not possess the constraints associated with those of Model 1 and Model 1*. The symptoms of nonmixing are certainly more definitively expressed in the residuals of an IR model, since the values in the (1,1) and (I,I) cells (when $I = J$) need not be zero. Also, the freedom of nonzero “never seen again” residuals allows the IR models to accurately capture the row patterns in the residuals matrix that emerge when cohort-specific problems are present.

The conclusions about the existence of patterns in model residuals for the simulated scenarios were based strictly on the sign of the value. It may also be possible to detect the same patterns and information pertaining to the relative magnitude of each residual by examining standardized residuals. For multiyear tagging models, a standardized residual is defined as $d_{ij} = (O_{ij} - E_{ij}) / \sqrt{E_{ij}(1 - E_{ij}/N_{ij})}$, where O_{ij} and E_{ij} represent the observed and fitted values, respectively. Consideration of the relative magnitude of model residuals can assist with the detection of outliers. If a model fits a particular data set well, then the standardized residuals should only rarely be greater than 2–3. Many large standardized residuals is indicative of overdispersion. If the variance in the data is greater than the theoretical variance predicted by the multinomial distribution, then overdispersion is present. This implies that the calculated standard errors generated from software packages for the analysis of tagging data (e.g., programs SURVIV and MARK) are generally overly optimistic about precision.

Examination of the residuals associated with the analysis of each striped bass recovery matrix revealed the presence of cohort-specific problems. The nonzero “never seen again” residuals in rows 1 and 2 of each residuals matrix were caused by the same counterintuitive trend. For each stock, approximately the same or fewer tags were recovered from the 1989 cohort than from the 1988 cohort even though significantly more fish were tagged in 1989. Based on the data, it appears that the number of striped bass effectively tagged in each state is substantially different from the actual number tagged in 1989. The most obvious explanation is short-term tagging mortality and (or) tag loss, and since the striped bass tagging program began in 1988, it is possible that inexperience with the sampling and tagging procedures (which would likely be present for all state agencies) allowed these phenomena to be present in the study. An alternative explanation is that perhaps the natural mortality rate of the fishes tagged in 1989 increased substantially due to some type of large-scale cohort-specific environmental or biological effect.

Acknowledgements

We gratefully acknowledge the continuing efforts of the Anadromous Fishes Research Program of the Virginia Institute of Marine Science who tag and release striped bass in Virginia’s rivers. We thank Carl Walters and two anonymous

reviewers for their helpful comments. This research was funded by the Wallop-Breaux Program of the U.S. Fish and Wildlife Service through the Recreational Fishing Advisory Board of the Virginia Marine Resources Commission (grant No. F-77-R-12). K.H. Pollock was supported by the South Carolina Department of Natural Resources (grant No. NA77FL0290). This is Virginia Institute of Marine Science contribution No. 2383.

References

- Akaike, H. 1973. Information theory as an extension of the maximum likelihood principle. *In* Second International Symposium on Information Theory. *Edited by* B.N. Petrov and F. Csaki. Akademiai Kiado, Budapest, Hungary.
- Akaike, H. 1985. Prediction and entropy. *In* A celebration of statistics. *Edited by* A.C. Atkinson and S.E. Fienberg. Springer, New York.
- Bertignac, M., Hampton, J., and Coan, A.L., Jr. 1999. Estimates of exploitation rates for north Pacific albacore, *Thunnus alalunga*, from tagging data. *Fish. Bull. U.S.* **97**: 421–433.
- Brownie, C., Anderson, D.R., Burnham, K.P., and Robson, D.S. 1985. Statistical inference from band recovery data: a handbook. 2nd ed. U.S. Fish Wildl. Serv. Resour. Publ. No. 156.
- Buckland, S.T., Burnham, K.P., and Augustin, N.H. 1997. Model selection: an integral part of inference. *Biometrics*, **53**: 603–618.
- Burnham, K.P., and Anderson, D.R. 1992. Data-based selection of an appropriate biological model: the key to modern data analysis. *In* *Wildlife 2001: populations*. *Edited by* D.R. McCullough and R.H. Barrett. Elsevier Science Publishers, London, U.K.
- Burnham, K.P., and Anderson, D.R. 1998. Model selection and inference: a practical information theoretical approach. Springer-Verlag, New York.
- Burnham, K.P., White, G.C., and Anderson, D.R. 1995. Model selection strategy in the analysis of capture–recapture data. *Biometrics*, **51**: 888–898.
- Henderson-Arzapalo, A., Rago, P., Skjveland, J., Mangold, M., Washington, P., Howe, J., and King, T. 1999. An evaluation of six internal anchor tags for tagging juvenile striped bass. *N. Am. J. Fish. Manage.* **19**: 482–493.
- Hoenig, J.M., Barrowman, N.J., Hearn, W.S., and Pollock, K.H. 1998a. Multiyear tagging studies incorporating fishing effort data. *Can. J. Fish. Aquat. Sci.* **55**: 1466–1476.
- Hoenig, J.M., Barrowman, N.J., Pollock, K.H., Brooks, E.N., Hearn, W.S., and Polacheck, T. 1998b. Models for tagging data that allow for incomplete mixing of newly tagged animals. *Can. J. Fish. Aquat. Sci.* **55**: 1477–1483.
- Larson, S.C., Saul, B., and Schleiger, S. 1991. Exploitation and survival of black crappies in three Georgia reservoirs. *N. Am. J. Fish. Manage.* **11**: 604–613.
- Latour, R.J., Pollock, K.H., Wenner, C.A., and Hoenig, J.M. 2001a. Estimates of fishing and natural mortality for red drum *Sciaenops ocellatus* in South Carolina waters. *N. Am. J. Fish. Manage.* In press.
- Latour, R.J., Hoenig, J.M., Olney, J.E., and Pollock, K.H. 2001b. A simple test for nonmixing in multi-year tagging studies: application to striped bass tagged in the Rappahannock River. *Trans. Am. Fish. Soc.* **130**: 848–856.
- Pollock, K.H., Hoenig, J.M., and Jones, C.M. 1991. Estimation of fishing and natural mortality when a tagging study is combined with a creel survey or port sampling. *Am. Fish. Soc. Symp.* **12**: 423–434.
- Pollock, K.H., Hoenig, J.M., Hearn, W.S., and Calingaert, B. 2001. Tag reporting rate estimation: an evaluation of the reward tagging method. *N. Am. J. Fish. Manage.* In press.
- Ricker, W.E. 1975. Computation and interpretation of biological statistics of fish populations. *Bull. Fish. Res. Board Can.* No. 191.
- Robson, D.S., and Youngs, W.D. 1971. Statistical analysis of reported tag recaptures in the harvest from an exploited population. *Biometrics Unit Mimeo. Ser. Pap. No. BU-369-M*. Cornell University, Ithaca, N.Y.
- Ross, J.L., Stevens, T.M., and Vaughan, D.S. 1995. Age, growth, mortality, and reproductive biology of red drums in North Carolina waters. *Trans. Am. Fish. Soc.* **124**: 137–154.
- Seber, G.A.F. 1970. Estimating time-specific survival and reporting rates for adult birds from band returns. *Biometrika*, **57**: 313–318.
- Smith, D.R., Burnham, K.P., Kahn, D.M., He, X., Goshorn, C.J., Hattala, K.A., and Kahnle, A.W. 2000. Bias in survival estimates from tag-recovery models where catch-and-release is common, with an example from Atlantic striped bass (*Morone saxatilis*). *Can. J. Fish. Aquat. Sci.* **57**: 886–897.
- White, G.C. 1983. Numerical estimation of survival rates from band-recovery and biotelemetry data. *J. Wildl. Manage.* **47**: 716–728.
- White, G.C., and Burnham, K.P. 1999. Program MARK — survival estimation from populations of marked animals. *Bird Study*, **46**: 120–138.
- Youngs, W.D., and Robson, D.S. 1975. Estimating survival rates from tag returns: model tests and sample size denominations. *J. Fish. Res. Board Can.* **32**: 2365–2371.