

## A Statistical, Age-Structured, Life-History-Based Stock Assessment Model for Anadromous *Alosa*

A. JAMIE F. GIBSON<sup>1</sup>

Acadia Centre for Estuarine Research, Post Office Box 115, Acadia University,  
Wolfville, Nova Scotia BOP 1X0, Canada; and Department of Biology,  
Dalhousie University, Halifax, Nova Scotia B3H 3J5, Canada

RANSOM A. MYERS<sup>2</sup>

Department of Biology, Dalhousie University,  
Halifax, Nova Scotia B3H 3J5, Canada

**Abstract.**—We present a population dynamics model based on the life history of anadromous *Alosa*. The model is built around a catch-at-age array to which we have added an additional dimension to include previous spawning history. The previous spawning history determines the number of times that a fish is exposed to riverine impacts that contribute to overall mortality rates. The model is designed to incorporate the kinds of data typically collected for anadromous *Alosa* stocks, such as catch-at-age data, spawning escapement counts at fish ladders, larval and juvenile abundance indices, and turbine mortality estimates. We show how the model can be adapted to individual stocks and management questions and how the model parameter estimates can be obtained using maximum likelihood. We demonstrate this approach with examples for two alewife *Alosa pseudoharengus* populations in Nova Scotia.

### Introduction

The biology, fisheries, and data for anadromous *Alosa* populations differ from those of marine fish. Consequentially, traditional fisheries models that are designed for marine species are often not appropriate for *Alosa* and do not fully utilize the available data. For example, riverine fisheries target only mature fish whose availability to the fishery depends not only on recruitment and mortality rates but also on variable maturity schedules. Additionally, anadromous fish are often affected by other anthropogenic activities such as hydroelectric generation and barriers (Rulifson 1994), and survivorship differs depending upon whether or not a fish is sexually mature and how many times it has previous spawned. A fish's previous spawning history is available from its scales (Marcy 1969). This information can therefore be included in the model and used to separate marine sources of mortality (a function of age), from riverine sources of mortality (a function of previous spawning history). Auxiliary data such as escapement counts at fish

ladders, larval abundance indices, and counts of seaward migrating juveniles are often available and can also be incorporated into an assessment model.

Fournier and Archibald (1982) and Deriso et al. (1985) developed the general theory for statistical catch-at-age models for stock assessment that allow auxiliary data to be incorporated into the model. With the development of software that allows complex, nonlinear models to be fitted rapidly, these techniques are being used more frequently for stock assessment. Here, we present an age-structured, life history model for anadromous *Alosa* and show how it can be linked to the kinds of data typically collected for *Alosa* stocks. This approach provides a flexible, dynamic framework for *Alosa* stock assessment and can be used to address critical management issues.

### The Model

The following model is based on the life cycles of the three species of anadromous *Alosa* that are indigenous to eastern North America: American shad *A. sapidissima*, blueback herring *A. aestivalis*, and alewife *A. pseudoharengus*. Although differences exist among species and among populations of the same species, the life cycles of anadromous *Alosa* have several shared characteristics. Adults of these species ascend rivers during the spring and spawn

<sup>1</sup>Corresponding author: gibsonajf@dfp-mpo.gc.ca;  
present address: Department of Fisheries and Oceans,  
Diadromous Fish Division, Science Branch, Post Office  
Box 1006, Dartmouth, Nova Scotia B2Y 4A2, Canada.

<sup>2</sup>E-mail: Ransom.Myers@dal.ca

in lakes, pools, or still waters within the watershed. Young of the year remain in freshwater until mid-summer to late fall when they emigrate to the sea. Fish mature at 2–7 years of age, and maturity schedules vary among populations and among years. Most populations are iteroparous. Stocks are often fished during the spawning migration, although intercept fisheries exist in some regions. Leggett and Carscadden (1978) describe the life history of American shad in greater detail, while Loesch (1987) provides an overview of the life histories of blueback herring and alewife. We model this life history as explained below.

Of primary interest is the number of fish of sex  $s$  (indexed “m” for male or “f” for female), age  $a$ , that have spawned  $p$  times previously and are returning to the river in year  $t$ , which we denote as  $N_{t,s,a,p}$ . Assuming a nonselective fishery, the number of eggs produced in year  $t$  ( $Q_t$ ) is a function of the number of females in year  $t$  ( $N_{t,f,a,p}$ ), the exploitation rate in that year ( $u_t$ ), and an age and previous spawning-specific fecundity ( $f_{a,p}$ ) and is given by

$$Q_t = \sum_{a,p} N_{t,f,a,p} (1 - u_t) f_{a,p}.$$

Density-dependent natural mortality within the spawning and nursery areas is thought to regulate *Alosa* population size (e.g., Crecco and Savoy 1987). This is to say that the rate of larval natural mortality ( $M_t^{\text{larval}}$ ) varies among years as a density-dependent function of  $Q_t$ . We write this as  $M_t^{\text{larval}} = g(Q_t)$ , where  $g$  is the function that describes the nature of the density dependence. The effects of environmental variability ( $\epsilon_t$ ) can be incorporated into the model as deviates around the density-dependent relationship. Given the sex ratio ( $v_s$ ), the number of offspring of each sex that survive to migrate seaward in year  $t$  ( $O_{t,s}$ ) is then

$$O_{t,s} = Q_t e^{-g(Q_t) + \epsilon_t} v_s.$$

Two equations are used to model the number of fish in the spawning run in each age, sex, and previous spawning history category. For fish that have not previously spawned ( $p = 0$ ), the number of fish of sex  $s$  and age  $a$  entering the river to spawn (downstream of the fishery) in year  $t$  is

$$N_{t,s,a,0} = O_{t-a,s} e^{-T^{\text{juv}}} m_{t-a,s,a} e^{-M_a^{\text{juv}}}.$$

Here,  $T^{\text{juv}}$  is the instantaneous rate of turbine mortality for juvenile fish (zero for rivers that are not

developed for hydroelectric generation) and  $M^{\text{juv}}$  is the instantaneous natural mortality rate for immature fish at sea. The maturity schedule ( $m_{t-a,s,a}$ ) is the probability that a fish of sex  $s$  that is alive at age  $a$  will mature at age  $a$ . The maturity schedule may vary among cohorts, where the cohort year is given by  $t - a$ . For fish that have spawned previously, the number of fish of sex  $s$  and age  $a$  that spawned  $p$  times previously entering the river (downstream of the fishery) in year  $t$  is

$$N_{t,s,a,p} = N_{t-p,s,a-p,0} e^{-\left(\sum_{k=t-p+1}^t F_k + T^{\text{adult}} p + M_{s,a}^{\text{adult}} p\right)},$$

where  $F$  is the instantaneous rate of fishing mortality,  $T^{\text{adult}}$  is the instantaneous rate of turbine mortality for adult fish, and  $M_{s,a}^{\text{adult}}$  is the sex- and age-specific instantaneous rate of natural mortality for adults (the relationship between  $F$  and the annual exploitation rate  $u$  is  $F_t = -\log_e[1 - u_t]$ ). Female spawner biomass (SSB) can be used as a proxy for the number of eggs if fecundity is directly proportional to weight:

$$\text{SSB}_t = \sum_{a,p} N_{t,f,a,p} w_{t,f,a,p} e^{-F_t}.$$

Overcompensation does not appear to be characteristic of *Alosa* populations (Gibson and Myers 2003, this volume), and we therefore assume a Beverton–Holt relationship between  $\text{SSB}_t$  and  $O_t$  (Hilborn and Walters 1992). This is a two-parameter spawner–recruit model where  $\alpha$  is number of recruits produced annually per unit biomass of spawners (Myers et al. 1999) and  $K$  is the half-saturation constant. The full dynamic model becomes

$$N_{t,s,a,p} = \begin{cases} \frac{\alpha \text{SSB}_{t-a}}{(1 + \text{SSB}_{t-a} / K)} e^{T^{\text{juv}}} v_s m_{t-a,s,a} e^{\frac{1}{2} M^{\text{juv}} a} & \text{if } p = 0 \\ N_{t-p,s,a-p,0} e^{-\left(\sum_{k=t-p+1}^t F_k + T^{\text{adult}} p + M_{s,a}^{\text{adult}} p\right)} & \text{if } p > 0 \end{cases}.$$

Two examples of how this model can be adapted to different populations are given below. The model is adapted to produce estimates for variables corresponding to the data that exists for the population. Model parameters are then estimated through minimization of the value of an objective function that relates the model predictions to the observed age structure, catch, and any auxiliary information (e.g., larval indices, escapement counts) that may exist for the population.

We programmed this model using AD Model Builder (Fournier 1996). AD Model Builder uses the

C++ auto-differentiation library for rapid fitting of complex nonlinear models, has Bayesian and profile likelihood capabilities, and is designed specifically for fitting these types of models.

**Example 1: Margaree River, Nova Scotia, Alewife**

The Margaree River in Nova Scotia supports an *Alosa* fishery that is executed in-river using tip traps installed along the bank (Chaput et al. 2001). Alewives are the dominant component of the catch. Exploitation rates are controlled using within-season closures that were first implemented in 1984 and have been subsequently modified. After 1995 it was evident that the population size had declined, and further closures were therefore introduced in 1996. Here, our objective is to use the model to determine whether this strategy successfully reduced exploitation rates to target levels of about 33% (Chaput et al. 2001).

The data for the Margaree River alewife fishery consists of the total catch ( $C_t$ ) for the years 1983–2000, an estimate of the number of fish captured in each age and previous spawning history category ( $C_{t,a,p}$ ) for the years 1983–2000, and a larval abundance index ( $I_t$ ) for the years 1983–1985 and 1989–2000. The larval index is based on the number of yolk sac larvae captured using a plankton net and is assumed to be measured before compensation occurs in the population. Based on this assumption, it is used as an index of spawner escapement. We use only the second half ( $P > 0$ ) of the full dy-

namics model. The model (Table 1) is set up as a combined sex model that estimates the number of virgin fish in each age-class that enter the river in each year ( $N_{t-p,a-p,0}$ ), the exploitation rate in each year, and a catchability coefficient for larval alewife ( $q$ ) for a total of 108 estimated parameters. This approach is similar to traditional statistical catch-at-age models (Quinn and Deriso 1999) except the previous spawning history is incorporated into the model by adding another dimension to the catch-at-age array. This increases the number of observations of total mortality rates in each year. We assumed a constant value of 0.6 for  $M^{\text{adult}}$  for all year- and age-classes. While this value is lower than that assumed by some other authors (e.g., Crecco and Gibson [1990] used  $M^{\text{adult}} = 1.0$ ), we have estimated nonfishing mortality on rivers where natural mortality is confounded with turbine mortality and obtained values close to 0.6. We assumed the larval index in year  $t$  was linearly related to spawning escapement in year  $t$  through a catchability coefficient (also assumed constant across years). We used a lognormal error structure for the catch ( $C_t^{\text{obs}}$  and  $C_t^{\text{pred}}$  are the observed and predicted catches in year  $t$ ) and the larval index ( $I_t^{\text{obs}}$  and  $I_t^{\text{pred}}$  are the observed and predicted larval indices in year  $t$ ). We used a multinomial error structure for the number of fish in each year, age, and previous spawning category ( $\pi_{t,a,p}^{\text{obs}}$  is the number of fish of age  $a$  that have spawned  $p$  times previously within a sample collected in year  $t$ , and  $p_{t,a,p}^{\text{pred}}$

Table 1.—The equations used for the Margaree River alewife model.

| Type of equation                        | Equation   |
|---|--|
| Dynamics                                | $N_{t,a,p} = N_{t-p,a-p,0} e^{-\left(\sum_{k=t-p+1}^t F_k + M_p^{\text{adult}}\right)}$ $C_{t,a,p} = N_{t,a,p} u_t$ $C_t = \sum_a \sum_p (N_{t,a,p} u_t)$ $I_t = q \sum_a \sum_p [N_{t,a,p} (1 - u_t)]$  |
| Log-likelihoods (non-constant portions) | $\ell_{\text{catch}} = -\sum_t (\log_e C_t^{\text{obs}} - \log_e C_t^{\text{pred}})^2$ $\ell_{\text{composition}} = -\sum_t \sum_a \sum_p \pi_{t,a,p}^{\text{obs}} \log_e p_{t,a,p}^{\text{pred}}$ $\ell_{\text{larval}} = -\sum_t (\log_e I_t^{\text{obs}} - \log_e I_t^{\text{pred}})^2$ |
| Objective function                      | $\text{OBV} = -(\lambda_1 \ell_{\text{composition}} + \lambda_2 \ell_{\text{catch}} + \lambda_3 \ell_{\text{larval}})$   |

is the predicted proportion of fish in each age and previous spawning category in that year). We fit the model by minimizing the value of an objective function that is the sum of the negative log-likelihoods for the catch, larval index, and number of fish in each year-age-previous spawning category. The relative contribution of each likelihood to the objective function was controlled by a set of weighting values ( $\lambda_i$ ) selected to keep any one part of the objective function from dominating the fit. Because of difficulties interpreting juvenile (Jessop 1994) and larval abundance indices, we weighted the larval index so that its contribution was about one half that of the other components.

The core of the model is shown in Figure 1. The catch is partitioned by cohort and age at maturity, and the abundance of fish in each category is projected through time. As shown in Figure 1, cohort sizes and the proportions maturing at each age vary among year-classes. Exploitation rates and the number of virgin fish in each age category are estimated in the model, and predicted catches and spawning escapements (Figure 2) are calculated from model output. The fit to the larval index is not as good as the fit to the catch or composition data because of the smaller weighting factor used for these data. The increased within-season closures have reduced exploitation rates from an average of 0.79 (1991–1995 time period) to 0.39 (1996–2000). Spawning escapement has increased as a result of these closures.

*Example 2: The Gaspereau River, Nova Scotia, Alewife Fishery*

The Gaspereau River, also in Nova Scotia, supports an alewife population that shows the characteristics of a heavily impacted stock (Gibson and Myers 2001). The stock is fished commercially as fish ascend the river to spawn, and the watershed has been extensively modified for hydroelectric generation. Water management policies are being developed to reduce impacts on this population, including improvements to fish passage facilities. Here, our objective was to use the life history model to determine the biomass of fish that need to reach the spawning areas to produce maximum sustainable yield ( $SSB_{MSY}$ ) in the fishery.

Data for the Gaspereau River alewife stock and fishery are limited. The data consist of the catches for the years 1964–2000 (we use 1979–2000 in this model because of uncertainty in the process that resulted in large catches in the mid-1970s); spawning escapement counts ( $E_i$ ) at a fish ladder just

upriver from the fishery for the years 1982–1984, 1995, and 1997–2000; and the sex, age, and spawning history composition for all years when counts were conducted except 1995 (Gibson and Myers 2001). We set up the model (Table 2) to estimate the log of the mean asymptotic recruitment ( $R_0$ ) and a recruitment deviate ( $\epsilon_i$ ) for each year around the spawner–recruit relationship. Mean asymptotic recruitment can be interpreted as the median carrying capacity of the nursery areas rescaled by survival to the age at recruitment, selected here as age 3. As such, all factors affecting survival from the egg to age 3 are incorporated into the spawner–recruit relationship. We used a logarithmic form of the Beverton–Holt model, parameterized in terms of  $R_0$ , using the substitution  $K = R_0/\alpha$ . The logarithmic form constrains recruitment to be positive during the estimation process and results in a multiplicative error structure for recruitment.

The  $SSB_{MSY}$  can be estimated from the spawner–recruit relationship. For semelparous species, given a spawner–recruit function  $R = f(S)$ , the spawning escapement at the maximum sustainable yield (MSY) occurs where  $f'(S) = 1$  (Quinn and Deriso 1999). For an iteroparous species, if fishing occurs just before spawning, natural mortality during the fishing season is negligible, the fishery is nonselective, and fish are fully grown when entering the fishery, the situation is analogous. The  $SSB_{MSY}$  occurs at the point where the first derivative of the spawner–recruit relationship equals the inverse of the rate at which recruits produce replacement spawners in the absence of fishing mortality, denoted as  $SPR_{F=0}$  (Gibson and Myers 2003):

$$f'(S) = \frac{1}{SPR_{F=0}}.$$

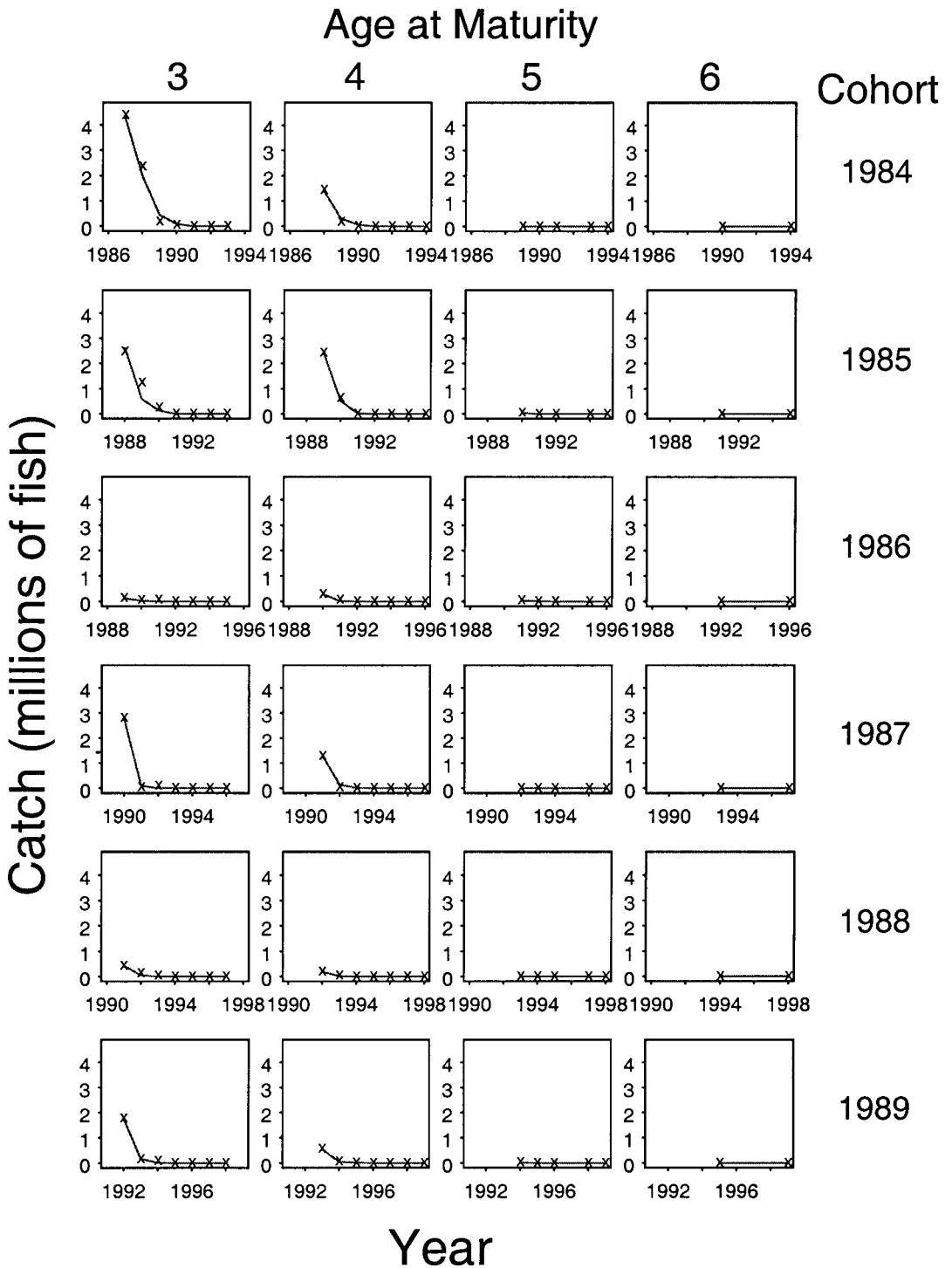
When fishing occurs on fish that are not fully grown, this relationship underestimates the true  $SSB_{MSY}$  (Deriso 1980). For the Beverton–Holt spawner–recruit model,

$$f'(S) = \frac{\alpha}{(1 + SSB_{MSY}/K)^2}.$$

Thus,

$$SSB_{MSY} = K\sqrt{SPR_{F=0}\alpha} - K.$$

Because the data for this population are very limited, a number of restrictive assumptions are made. Foremost, we treat the exploitation rate as



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Figure 1.—Part of the observed (x) and predicted (lines) catch-at-age arrays for the Margaree River, Nova Scotia, alewife population. Catches are partitioned by cohort year (right column) and age at maturity (top labels). The year (bottom labels) is the year of capture.

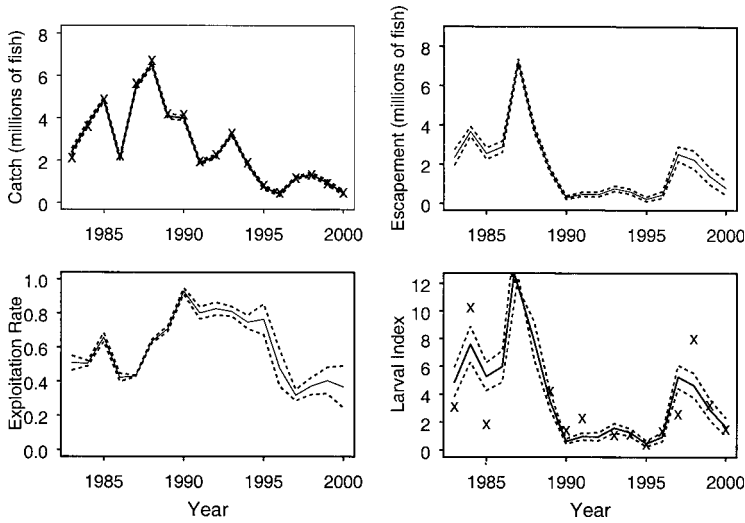


Figure 2.—Observed (×) and predicted (solid lines) total catches and larval indices and predicted exploitation rates and spawning escapements for the Margaree River, Nova Scotia, alewife population. The dashed lines show 95% confidence intervals for the estimated values based on normal approximations.

Table 2.—The equations used for the Gaspereau River alewife model.

| Type of equation                        | Equation   |
|---|--|
| Dynamics                                | $\log_e R_t = \log_e(\alpha) + \log_e(SSB_{t-3}) - \log_e \left[ 1 + \left( \frac{SSB_t}{R_0 / \alpha} \right) + \varepsilon_t \right]$ $N_{t,s,a,0} = R_{t-a+3} v_s m_{s,a} e^{-M^{juv}(a-3)}$ $C_{t,s,a,p} = N_{t,s,a,p} u_t$ $C_t = \sum_s \sum_a \sum_p (N_{t,s,a,p} u_t)$ $E_{t,s,a,p} = N_{t,s,a,p} (1 - u_t)$ $N_{t+1,s,a+1,p+1} = E_{t,s,a,p} e^{-M^{adult}}$ $SSB_t = \sum_s \sum_a \sum_p (E_{t,s,a,p} w_{t,s,a,p})$ |
| Reference point                         | $SSB_{MSY} = K \sqrt{SPR_{F=0} \alpha} - K$  |
| Log-likelihoods (non-constant portions) | $\ell_{catch} = -\sum_t (\log_e C_t^{obs} - \log_e C_t^{pred})^2$ $\ell_{composition} = -\sum_t \sum_s \sum_a \sum_p \pi_{t,s,a,p}^{obs} \log_e P_{t,s,a,p}^{pred}$ $\ell_{escapement} = -\sum_t (\log_e E_t^{obs} - \log_e E_t^{pred})^2$   |
| Objective function                      | $OBV = -(\lambda_1 \ell_{composition} + \lambda_2 \ell_{catch} + \lambda_3 \ell_{escapement})$   |

known. For years where the catch and spawning escapement are known, the exploitation rate can be calculated directly. We use the mean exploitation rate for years that lack escapement counts. We also treat the maturity schedule as fixed across cohorts. While this assumption is not realistic, the data are insufficient to estimate a maturity schedule for each cohort (we only have age data for 7 of the 21 years). We fixed  $\alpha = 60.7$  (at low spawner abundance, 1 kg of spawners can produce 60.7 age-3 recruits annually). This value was taken from a meta-analysis of five other populations (Gibson and Myers 2001). As in the previous example, we fit the model to the data by minimizing an objective function value that is the weighted sum of the nonconstant portions of the negative log-likelihoods of the catches, escapement counts, and sex-age-previous spawning compositions of the spawning run.

While the estimated recruitment deviates for each year have wide standard errors (Table 3), the mean asymptotic recruitment and the spawning biomass at MSY are well determined by the model. These reference points are consistent with those produced by a meta-analysis of alewife populations (Gibson and Myers 2001). As weighted, the model tracks the count very closely (Figure 3) and fits the catch reasonably well except during the 1984–1988 time period. We believe the large residuals in this time period may be due to annual variability in the maturity schedules and the possibility that the mean exploitation rate may not be indicative of the exploitation rates in these years. However, we simply do not have the data to investigate these hypotheses; only the catch is known during this time period. The estimated  $SSB_{MSY}$  implies that MSY occurs with an equilibrium spawner abundance of about 400,000 fish. Current spawner abundance is typically 10–40% of this level. The mean asymptotic recruitment for this population is about 1.7 million fish. The estimated recruitment is lower than this value in 14 of the 19 years that were included in the model.

## Discussion

In this paper, we have presented a general, life-history-based model for the population dynamics of anadromous *Alosa* and shown how the model can be used for stock assessment by adapting it to the data collected for individual populations. This approach has several advantages, the foremost being that the life history of interest is specifically modeled. For *Alosa*, data such as spawning escape-

Table 3.—Parameter estimates for the Gaspereau River alewife population obtained from the statistical life history model. While the standard errors for the recruitment deviates are large relative to their estimates, the mean asymptotic recruitment ( $R_0$ ; number of fish) and spawning biomass ( $SSB_{MSY}$ ; kg) at maximum sustainable yield are comparatively well estimated.

| Year and variable | Recruitment deviate | Standard error |
|-------------------|---------------------|----------------|
| 1979              | -0.81               | 1.49           |
| 1980              | -0.81               | 1.51           |
| 1981              | -0.81               | 1.51           |
| 1982              | -0.38               | 0.99           |
| 1983              | 0.93                | 0.61           |
| 1984              | -0.81               | 2.12           |
| 1985              | 1.49                | 0.01           |
| 1986              | 0.29                | 0.93           |
| 1987              | -1.43               | 0.16           |
| 1988              | 1.45                | 0.08           |
| 1989              | -0.04               | 2.09           |
| 1990              | -1.09               | 1.16           |
| 1991              | 0.43                | 0.60           |
| 1992              | 0.88                | 0.83           |
| 1993              | 0.56                | 1.17           |
| 1994              | 0.60                | 2.46           |
| 1995              | 1.07                | 1.36           |
| 1996              | -0.82               | 1.04           |
| 1997              | -0.35               | 1.50           |
| 1998              | 0.12                | 0.59           |
| 1999              | 0.32                | 1.50           |
| 2000              | -0.81               | 0.59           |
| $R_0$             | 1,647,800           | 602,330        |
| $SSB_{MSY}$       | 91,939              | 33,607         |

ment counts at fish ladders, larval and juvenile abundance indices, counts of emigrating juveniles, previous spawning history, indices of the number of postspawning fish (Olney and Hoenig 2001), and information about other sources of mortality can be incorporated into the assessment process.

One of the most useful pieces of information often collected for *Alosa* that is not typically available for marine species is the number of times that a fish has previously spawned (available from a fish's scales). Riverine impacts such as fishing or turbine passage do not affect immature fish at sea. When the number of times a fish has previously spawned is known, this variable can be used to determine the number of times that the fish has been exposed to riverine impacts by adding an extra dimension to the catch-at-age array. Additionally, when data are partitioned by sex and age at maturity as well as age, the number of observations of a cohort each year increases (from one to eight for a population that matures over 4 years). Assuming an adequate sample size, this increase

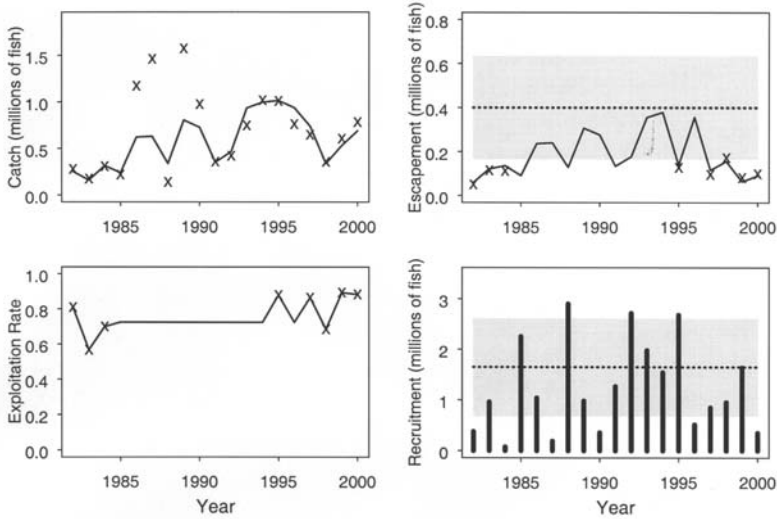


Figure 3.—Observed (x) and predicted (lines) total catches and spawner escapement counts and the exploitation rates (assumed known) and predicted number of age-3 recruits for the Gaspereau River, Nova Scotia, alewife population. The dashed lines show the number of spawners at maximum sustainable yield (upper right panel) and the median asymptotic recruitment (lower right panel) for this population. The gray shaded areas are 90% confidence intervals for these reference points.

improves the researcher's ability to estimate mortality rates or other parameters that are held constant across these categories.

While not specific to *Alosa* populations, statistical methods of fitting stock assessment models have a major advantage over virtual population analyses: models can be fit to intermittent data sets. For many smaller fisheries, such as the Gaspereau River example presented here, assessment data are not collected each year. Virtual population analysis-based methods use a backward summation for which estimates of the numbers at age are required for each year (Hilborn and Walters 1992). While fitting through long periods when age data were not collected requires that additional constraints be placed on the model, statistical methods can be used to estimate abundance when all that is known is the size of the catch.

Our life history model can be further generalized where appropriate for some populations. As presented, we have treated *Alosa* fisheries as non-selective. When selective fishing gear such as gill nets are used, selectivity models (e.g., Millar and Holst 1997) can be incorporated into our framework, allowing the error in the selectivity parameter estimation to be carried forward through the assessment. Similarly, when catchability varies with fish abundance (e.g., Harley et al. 2001), these relationships can also be included in the model.

Meta-analytic approaches to stock assessment and fisheries biology are becoming more common (e.g., Myers et al. 1999; Gibson and Myers 2003). In order for these approaches to be successful, some standardization among data sets (e.g., a standard definition of recruitment for spawner–recruit meta-analysis) is required. When a general life history model is used for the assessments, a basis for these kinds of standardizations is provided.

At present, we have not generalized our computer code so that it can be applied to a generic stock. The modeling framework is intended to be flexible and to be adapted to the data and biology of specific populations. Thus far, we have fit the model to four alewife populations, each with different kinds of data. The computer code, and assistance with adapting it to other populations, is available from the authors.

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## References

- Chaput, G., P. LeBlanc, and R. Crawford. 2001. Assessment of the Margaree River gaspereau fishery, 1997 to 2000. Department of Fisheries and Oceans, Canadian Stock Assessment Secretariat Research Document 2001/046.
- Crecco, V., and T. Savoy. 1987. Effects of climatic and density-dependent factors on intra-annual mortality of larval American shad. Pages 69–81 in R. D. Hoyt, editor. 10th annual larval fish conference. American Fisheries Society, Symposium 2, Bethesda, Maryland.
- Crecco, V. A., and M. Gibson. 1990. Stock assessment of river herring from selected Atlantic coast rivers. Atlantic States Marine Fisheries Commission, Special Report 19, Washington, D.C.
- Deriso, R. B. 1980. Harvesting strategies and parameter estimation for an age-structured model. Canadian Journal of Fisheries and Aquatic Sciences 37:268–282.
- Deriso, R. B., T. J. Quinn II., and P. R. Neal. 1985. Catch-age analysis with auxiliary information. Canadian Journal of Fisheries and Aquatic Sciences 42:815–824.
- Fournier, D. 1996. An introduction to AD Model Builder for use in nonlinear modelling and statistics. Otter Research Ltd., Nanaimo, British Columbia.
- Fournier, D. A., and C. P. Archibald. 1982. A general theory for analyzing catch at age data. Canadian Journal of Fisheries and Aquatic Sciences 39:1195–1207.
- Gibson, A. J. F., and R. A. Myers. 2001. Gaspereau River alewife stock status report. Department of Fisheries and Oceans, Canadian Stock Assessment Secretariat Research Document 2001/061.
- Gibson, A. J. F., and R. A. Myers. 2003. A meta-analysis of the habitat carrying capacity and the maximum reproductive rate of anadromous alewife in eastern North America. Pages 211–221 in K. E. Limburg and J. R. Waldman, editors. Biodiversity, status, and conservation of the world's shads. American Fisheries Society, Symposium 35, Bethesda, Maryland.
- Harley, S. J., R. A. Myers, and A. Dunn. 2001. Is catch-per-unit-effort proportional to abundance? Canadian Journal of Fisheries and Aquatic Sciences 58:1705–1772.
- Hilborn, R., and C. J. Walters. 1992. Quantitative fisheries stock assessment: choice, dynamics and uncertainty. Chapman and Hall, New York.
- Jessop, B. 1994. Relations between stock and environmental variables, and an index of abundance, for juvenile alewives and blueback herring. North American Journal of Fisheries Management 14:564–579.
- Leggett, W. C., and J. E. Carscadden. 1978. Latitudinal variation in the reproductive characteristics of American shad (*Alosa sapidissima*): evidence for population specific life history strategies in fish. Journal of the Fisheries Research Board of Canada 35:1469–1478.
- Loesch, J. G. 1987. Overview of the life history aspects of anadromous alewife and blueback herring in freshwater habitats. Pages 89–103 in M. J. Dadswell, R. J. Klauda, C. M. Moffitt, R. L. Saunders, R. A. Rulifson, and J. E. Cooper, editors. Common strategies of anadromous and catadromous fishes. American Fisheries Society, Symposium 1, Bethesda, Maryland.
- Marcy, B. C., Jr. 1969. Age determinations from scales of *Alosa pseudoharengus* (Wilson) and *Alosa aestivalis* (Mitchill) in Connecticut waters. Transactions of the American Fisheries Society 98:622–630.
- Millar, R. B., and R. Holst. 1997. Estimation of gillnet and hook selectivity using log-linear models. ICES Journal of Marine Science 54:471–477.
- Myers, R. A., K. G. Bowen, and N. J. Barrowman. 1999. The maximum reproductive rate of fish at low population sizes. Canadian Journal of Fisheries and Aquatic Sciences 56:2404–2419.
- Olney, J. E., and J. M. Hoenig. 2001. Managing a fishery under moratorium: assessment opportunities for Virginia's stocks on American shad. Fisheries 26(2):6–11.
- Quinn, T. J., and R. B. Deriso. 1999. Quantitative fish dynamics. Oxford University Press, New York.
- Rulifson, R. A. 1994. Status of anadromous *Alosa* along the east coast of North America. Pages 108–112 in J. E. Cooper, R. T. Eades, R. J. Klauda, and J. G. Loesch, editors. Anadromous *Alosa* symposium. American Fisheries Society, Tidewater Chapter, Bethesda, Maryland.

