Fisheries and Oceans Science | Pêches et Océans Sciences

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Research Document 2001/061 | **Document de recherche 2001/061**

Gaspereau river alewife stock status report.

Rapport sur l'état du stock de gaspareau de la rivière Gaspereau.

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ISSN 1480-4883
Ottawa, 2001

Canada

Abstract

The Gaspereau River watershed in Nova Scotia supports a stock of anadromous alewives (*Alosa pseudoharengus*) of local economic and ecological importance. The stock is fished both recreationally and commercially as it ascends the river to spawn during May and June, with an average value for the commercial catch of $288,000 per year (range: $24,000 to $1,000,000) between 1974 and 1999. Estimated fishery exploitation rates for this stock in 1999 and 2000 were 88.4% and 89.4% respectively, two of the highest rates recorded for this stock. The stock exhibits the characteristics of a heavily impacted stock: the majority of fish belong to only 2 age classes and the percentage of repeat spawners in 2000 was less than 10%. We suggest that the spawning escapement that provides maximum sustainable yield can be used as a reference point for this stock, and estimate that MSY occurs when around 400,000 to 450,000 reach Gaspereau Lake to spawn. Recent spawner escapements to Gaspereau Lake are about 10% to 20% this target. Under current water management practices, alewives are diverted past 4 of the 5 generating stations in the watershed. Mortality of alewives at the White Rock station is unknown. Spawning biomass and the catch at MSY decline in proportion to the level of juvenile passage mortality. The fishery is sustainable even at high levels of adult passage mortality, because the fish have an opportunity to reproduce prior to passage. We suggest that the hierarchical and life history models used to calculate target escapements in this report have significant potential as management tools, but need further development. Given adequate spawner abundance, current water management practices to protect alewives could be re-evaluated to allow greater flexibility in water use for other purposes.

Résumé

Le bassin hydrographique de la rivière Gaspereau, en Nouvelle-Écosse, abrite un stock de gaspareau anadrome (Alosa pseudoharengus) d'importance économique et écologique au niveau local. Ce stock est l'objet d'une pêche récréative et commerciale lorsque le gaspareau y revient frayer en mai et juin. La valeur moyenne des prises commerciales a atteint 288 000 $ par année (plage de 24 000 $ à 1 000 000 $) de 1974 à 1999. Les taux d'exploitation estimatifs de ce stock en 1999 et 2000 se situaient à 88,4 % et 89,4 %, respectivement, soit deux des taux les plus élevés qui aient été enregistrés jusqu'à maintenant. Le stock montre les caractéristiques d'un stock fortement surexploité : la plupart des poissons n'appartiennent qu'à deux classes d'âge et le pourcentage de gaspareaux à pontes antérieures en 2000 se chiffrait à moins de 10 %. Les auteurs sont d'avis que l'échappée donnant un rendement maximal soutenu peut servir de point de référence pour ce stock et estiment que ce rendement se manifeste lorsque environ 400 000 à 450 000 gaspareaux réusissent à atteindre le lac Gaspereau pour y frayer. Les récentes échappées au lac Gaspereau atteignent à peu près 10 à 20 % de cette cible. Selon les pratiques de gestion des eaux en vigueur, les gaspareaux contournent quatre des cinq centrales hydroélectriques du bassin versant. Le taux de mortalité des gaspareaux imputable à la centrale de White Rock est inconnu. La biomasse de géniteurs et les prises au RMS diminuent en proportion du taux de mortalité des juvéniles due à leur passage. La pêche est durable même à des taux de mortalité élevés des adultes dus au passage parce qu'ils peuvent frayer avant de passer. Les auteurs considèrent que les modèles hiérarchiques et les modèles du cycle vital utilisés pour calculer les échappées cibles dans le présent rapport sont prometteurs comme outils de gestion, bien qu'ils doivent être raffinés. Si l'abondance des géniteurs est adéquate, les pratiques de gestion des eaux en vigueur visant à protéger le gaspareau pourraient être réévaluées de sorte à permettre une utilisation des eaux à d'autres fins.

1. INTRODUCTION

1.1 Background

The Black River - Gaspereau River watershed in Nova Scotia supports a stock of anadromous alewives (*Alosa pseudoharengus*) of local economic and ecological importance. The stock is fished both recreationally and commercially as it ascends the river to spawn during May and June, with an average value for the commercial catch of $288,000 per year (range: $24,000 to $1,000,000) between 1974 and 1999. Ecologically, they are an important prey species at sea and in fresh water, are predators that can alter zooplankton community composition within lakes (Mills *et al.* 1992), and serve as a vector for nutrient transport from the oceans to inland waters (Garman 1992).

Adults of this species spawn in fresh water in the spring, returning to the sea shortly thereafter. Spawning occurs in headwater lakes, stillwaters and back eddies, and eggs hatch after 3 to 8 days at Nova Scotia ambient temperatures. Young-of-the-year (YOY) remain in fresh water until mid-summer or fall, at which time they migrate to sea (Loesch 1987). Alewives then remain at sea until reaching sexual maturity after a period of 3 to 6 years. Alewives can live to over 10 years of age, and may spawn 5 or more times during their life. Over 100 rivers and streams in Nova Scotia support alewife stocks. While little information exists about many of these populations, the majority are thought to be in decline. In a review of the status of Alosa stocks in eastern North America, dams were identified as the primary factor responsible for this decline (Rulifson 1994).

The Black River - Gaspereau River watershed has been extensively modified for hydroelectric generation during the last 80 years. Modifications include diversions of the Black River, Gaspereau River, Forks River, and numerous smaller brooks and streams, most of which were completed by the early 1950's. Upgrades and minor changes to the system are ongoing. The system currently consists of over a dozen lakes interconnected by manmade canals and natural waterways (Figure 1). Five hydroelectric generating stations and numerous storage and diversion dams are present on the system. These structures affect fish migration and ecology within the watershed.

Nova Scotia Power Inc. (NSPI), in conjunction with government agencies, community groups and educational and research institutions, has been working towards reducing the impact of its activities upon local fish stocks. Fish ladders, diversion screens, spillways and control gates are used by NSPI to limit their impact on these stocks. The operation of these facilities is adjusted, as the ecology of these stocks is better understood. Water management strategies, designed to optimize water availability for other users as well as hydroelectric generation, are currently being tested.

Within the watershed, adult alewives typically ascend the watershed by way of the old Gaspereau River channel to spawn in lakes at the head of the system. Eggs hatch during late June and early July, and YOY then utilize these lakes as nursery areas prior to emigrating seaward during late summer and fall. YOY alewives tend to follow the dominant flow patterns when moving downstream. When the control gate at Forest Home

is closed, YOY alewives move seaward via the outlet from Gaspereau Lake to the Gaspereau River at Lanes Mill. When the control gate is open, YOY alewives also move downstream via Trout River Pond, were a diversion screen, located near its outlet redirects the fish back to the Gaspereau River via Trout River. In this way, fish are able to bypass 4 of the 5 generating stations in the watershed. As such, proper management of this control gate and the diversion screen are integral to the management of this species within the watershed. Currently, the control gate at Forest Home is closed when the adults enter Gaspereau Lake to spawn (c. early May), and re-opened after YOY are large enough that a diversion screen is effective (c. mid-August). The major storage reservoirs within this watershed are located upstream of the Forest Home control gate. The closure of this gate therefore places limits on water availability for hydroelectric generation or other uses during the closure. The timing and duration of this closure is therefore one of the key management issues within the watershed, affecting not only alewives, but all water resource users within the watershed.

With respect to alewives, the effectiveness of these strategies is evaluated through stock assessments (conducted intermittently throughout the last three decades), studies of YOY ecology in Gaspereau Lake, and by studying patterns of YOY outmigration at both Lanes Mill and at the diversion screen. Information about the performance of the fishery, life history data and stock size has been collected during stock assessments conducted by the federal Department of Fisheries and Oceans (DFO) between 1982 and 1984 (Jessop and Parker 1988), in 1995 by NSPI (unpublished data) and though a research collaboration between the Acadia Centre for Estuarine Research (ACER) and NSPI, between 1997 and 2000 (Gibson and Daborn 1997, Gibson 1999, Gibson 2000a, Gibson 2000b). Biological data relating to this stock were also collected during an evaluation of the fish ladder at White Rock in 1970 (Dominy 1971). During years when assessments were conducted, the spawning run has averaged c.537,000 fish (range: 165,000 to 1,082,000 fish). However, all assessments have been carried out in years when the catch was less than the 30 year median, and therefore do not accurately reflect the size of the stock. The stock is comprised mainly of first time spawners, 4 or 5 years of age. Fishing mortality undoubtedly contributes to this truncated age frequency distribution, as estimates of the exploitation rate have ranged from 56.7% in 1983 to 89.4% in 1999.

Some information exists about juvenile alewives in this watershed. Jessop and Parker (1988) monitored the distribution of YOY within the watershed during 1983. Information about the timing of outmigration and the size of migrating YOY was collected as part of an assessment of the Trout River Pond diversion screen during 1996 (Gibson 1996). During the summer and fall of 1997 (Gibson and Daborn 1998) and 1998 (Gibson 1999), the ecology of young-of-the-year alewives in Gaspereau Lake was studied to collect data useful for the development of management strategies for these fish. YOY alewives appear to be present in all regions of Gaspereau Lake throughout the summer. Larvae were present until the end of July. During these studies, alewives were large enough for the Trout River Lake diversion screen to be effective by mid-August. YOY alewives within Gaspereau Lake feed predominantly on calanoid copepods and smaller cladocerans (Lent 1999). Decreases in zooplankton abundance in Gaspereau Lake in early July, and bimodal YOY length frequency distributions throughout July and August

suggest that intraspecific competition may limit alewife reproductive success in this watershed.

1.2 Objectives

Data and analyses in this report are provided in three sections. The first section provides a summary of previous data collections pertaining to the status of the Gaspereau - Black River alewife stock and fishery. The data collected are comprehensive and allow direct calculation of annual stock sizes and exploitation rates. The status of the stock is therefore well known. More difficult is the selection and estimation of biological and fishery reference points for this stock, which is undertaken in two ways. A statistical catch-at-age/life history model is fitted to the catches, spawning escapements and age structure data from the first section. Model output is compared with a preliminary meta-analysis of stock-recruitment data for 5 other alewife stocks, also included in this report. Deficiencies in the data and the relationships between water management and management targets for fisheries are discussed as a basis for future research.

2. STOCK ASSESSMENTS

The record of the Gaspereau River alewife catch in the river extends from 1964 to 2000. Data are collected as the number of 50 lb pails of fish (c.115-130 fish/ pail, depending on their size) taken by the commercial and recreational fisheries downstream from the White Rock dam. It is unknown whether the high catches between 1975 and 1978 (Figure 2) were due to increased fishing effort as a result of a price increase for alewife, increased abundance due to strays from the Avon River as a result of the construction of the causeway, or some other factor. During this time period, the alewife catch in the Gaspereau River has averaged 7,120 pails (Table1).

Biological data to assess the status of the alewife stock have been collected during the years 1982 to 1984, 1995 and 1997 to 2000. Data were collected as fish ascended the fish ladder bypassing the White Rock generating station. Alewives were counted as they passed through a v-notch, counting weir located near the top of the ladder. During all years except 1995, the weir was closed to prevent fish passage when attendants were not present, ensuring a total count for those years. Alewife counts at White Rock have ranged from a low of 50,400 fish in 1982 to a high of 171,639 fish in 1998 (Table 2).

The number of fish per pail averaged 127 (n=6 pails) in 1997. We converted the catch in pails to the number of fish captured using this value standardized between years by the mean weight of the fish in each year. For a given year t, fishery exploitation rates (μ_t) were then calculated as:

$$\mu_t = \frac{Catch_t}{Catch_t + Count_t}$$

This method does not account for any fish that escape the fishery and do not ascend the ladder, resulting in an underestimation of stock size and an overestimation of the

exploitation rate. We do not believe this bias is large. For the years when counts are available (excluding the partial count in 1995), exploitation rates have averaged 78.6% (Table 2). The mean stock size from these assessments (about 537,000 fish) may not accurately reflect the true mean stock size because all counts occurred in years when the catch was below its 30 year median.

Partial counts of the alewives ascending the ladder into Gaspereau Lake at Lanes Mill were carried out during 1997 and 1998. Under the assumption that the daily migration pattern was similar at White Rock and Lanes Mills, we standardized the number of alewives counted at Lanes Mills by the proportion of the daily total at White Rock that were counted during the same time period. We estimated that 46.1 and 56.4% of the fish that ascended the White Rock ladder completed the migration to Lanes Mill in 1997 and 1998 respectively. Few larval alewives were captured during surveys in the Gaspereau River downstream of Lanes Mills during 1997, suggesting that reproduction downstream of Gaspereau Lake is not particularly successful. Additionally, larvae in the lower river were heavily parasitized by bivalve glochidia that almost certainly reduced the survival of these larvae. We therefore do not believe that reproduction downstream of Gaspereau Lake contributes significantly to this stock.

Sampling for morphometric data has varied between assessments. From 1982 to 1984, samples of 50 fish were dipped twice weekly from the fish ladder. From 1997 to 2000, 10 fish were randomly selected from every 1000 alewives that ascended the ladder. Fork length, weight and sex were recorded for each fish sampled. Scale samples were collected and used to determine age and previous spawning history.

The Gaspereau River alewife population exhibits the characteristics of a heavily impacted stock, including a truncated age distribution, and low percentage of repeat spawners (Table 3).

3. ESTIMATION OF BIOLOGICAL REFERENCE POINTS

We assume that year class strength of anadromous alewives is determined primarily through intra-specific competition occurring in the pre-migratory larval and juvenile life stages. This is to say that the carrying capacity of freshwater nursery areas is the factor that ultimately limits the size of an alewife stock. It follows that a fixed escapement policy that ensures adequate spawning escapement to fill these nursery areas is an ideal management strategy for alewife. In the Gaspereau River, fishing occurs downstream of the White Rock dam, and in any given year the size of the stock is not known until after fishing occurs. This renders a fixed escapement policy difficult to implement. Target fishing mortalities that ensure adequate spawning escapement in some portion of the years may therefore a more feasible management policy. However, without knowledge of mortality from other sources, this reference point cannot be calculated, and would also be difficult to implement without knowledge of the efficiency of the fishing gear. Here, we estimate three reference points to assist in the selection of management targets, the mean asymptotic recruitment (R_0), the equilibrium spawning stock biomass in the absence of fishing (SSB_{eq}) and the equilibrium spawning stock biomass at MSY (SSB_{msy}). We

estimate these parameters from analyses of the population dynamics of alewife, using a life history model tuned to the Gaspereau River, and a meta-analysis of 5 other alewife stocks, as outlined below.

3.1 Dynamics:

We model the population dyamics of alewives using two equations, a spawner-recruitment relationship that expresses recruitment as a function of spawner biomass, and the replacement line, the slope of which is the inverse of the rate at which recruits produce replacement spawners. The implicit assumption is made that all compensatory processes occur between spawning and recruitment. We therefore select the age of recruitment to be 3 (the earliest age of maturity), and define recruitment as:

$$R_t = \sum_{a=3}^{6} \left(N_{t+a,a,0} / e^{-M(a-3)} \right)$$

where $N_{t+a,a,0}$ is the number of fish of age a in year $t+a$ that have spawned 0 times previously, and M is the instantaneous rate of natural mortality for immature alewives at sea, assumed to be 0.4 in this report.

We assume that the functional form of the spawner-recruitment relationship is the Beverton-Holt model:

$$R_t = \frac{\alpha S_t}{1 + (S_t / \mathrm{K})}$$

where R_t is the number of recruits in year class t, S_t is the spawner biomass in year t, α is the slope of the S-R function at the origin (the mean annual maximum reproductive rate of the population at low population sizes) and K is the half-saturation constant (the spawner biomass corresponding to ½ the mean asymptotic recruitment (R_0). Here $R_0 = \alpha K$.

Given a constant natural mortality rate for mature and immature fish, the rate at which recruits produce spawning biomass in the absence of fishing ($SPR_{F=0}$) is:

$$SPR_{F=0} = \sum_{a_{rec}}^{\infty} q_a w_a e^{-M(a-a_{rec})}$$

where q_a is the probability that a fish is mature at age a, w_a is the mean weight at age a, and M is the instantaneous natural mortality rate. The situation is more complex, if the natural mortality rates differ for mature and immature fish. Here:

$$SPR_{F=0} = \sum_{a_{rec}}^{a_{max}} SS_a w_a$$

where SS_a is given by:

$$SS_3 = p_3$$

$$SS_4 = SS_3 e^{-M_{ad}} + (1-p_3)e^{-M_{juv}} p_4$$

$$SS_5 = SS_4 e^{-M_{ad}} + (1-p_3)(1-p_4)e^{-2M_{juv}} p_5$$

$$SS_6 = SS_5 e^{-M_{ad}} + (1-p_3)(1-p_4)(1-p_5)e^{-3M_{juv}} p_6$$

.

.

$$SS_{a_{\max}} = SS_{a_{\max}-1} e^{-M_{ad}} + (1-p_3)(1-p_4)...(1-p_{a_{\max}-1})e^{-(a_{\max}-3)M_{juv}} p_{a_{\max}}$$

Here, p_a is the probability that an immature fish that is alive at age a, matures at that age.

For semelparous species, given a spawner-recruit function $R=f(S)$ and $SPR_{F=0}=1$, the spawning escapement at 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 non-selective and fish are fully grown prior to entering the fishery, the situation is analogous. SSB_{msy} occurs where:

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

When fishing occurs when fish are not full grown, this relationship underestimates the true SSB_{msy} (Deriso 1980).

For the Beverton-Holt spawner-recruit model,

$$\frac{1}{SPR_{F=0}} = \frac{\alpha}{\left(1 + SSB_{msy}/K\right)^2}.$$

Thus,

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

Defining the mean lifetime maximum reproductive rate $\tilde{\alpha}$ (Myers et al. 1999) as the average rate at which replacement spawners are produced per spawner at low spawner abundance and in the absence of anthropogenic mortality:

$$\tilde{\alpha} = SPR_{F=0}\alpha$$

we can reparameterize the Beverton-Holt spawner-recruit model as a function of $\tilde{\alpha}$ and SSB_{msy}:

$$R_t = \frac{\tilde{\alpha} S_t}{1 + \left(\frac{S_t(\sqrt{\tilde{\alpha}} - 1)}{SSB_{msy}} \right)}$$

Under the assumptions above, this model allows estimation of SSB_{msy} directly from spawner-recruit time series.

3.2 Hierarchical Modelling

Traditionally, fisheries biologists have relied upon data only from the population of interest to assess the effects of pollution, fishing and other activities. Unfortunately, long and detailed time series are required to arrive at firm conclusions, and these time series simply do not exist for the majority of stocks (Myers and Mertz 1998). Fortunately many stocks of the same species, or closely related species, share similar life history strategies. For this reason, parameter estimates from several stocks can be combined, providing a distribution for parameter estimates at some higher organizational level (e.g. the species). This approach, known as hierarchical modelling, allows conclusions to be reached by drawing upon data from many stocks, thus reducing the uncertainty of biological parameters used in fisheries management (Myers and Mertz 1998). The resulting estimates can then be combined with comparatively limited stock-specific data to make inferences at the level of the specific stock. This approach has been used to study the maximum reproductive rates of fish populations (Myers *et al.* 1999) and the carrying capacity of the ocean for cod (Myers *et al*. in press). Here, we adapt the methods of Myers *et al*. (in press) to fit the model developed in the previous section to 5 alewife stocks simultaneously, providing mean estimates of the lifetime maximum reproductive rate and SSB_{msy} for alewife. These estimates are then used to make inferences of target spawning escapements for alewife in the Gaspereau River.

Statistical model:

We want to estimate SSB_{msy} for several alewife stocks simultaneously to allow for comparison of productivity across stocks and to provide an estimate of the mean productivity of alewife stocks that can be used as a guide for target spawning escapements in the absence of stock specific data. We adapt the methods of Myers *et al*. (in press) developed to estimate equilibrium spawning stock biomass, to our model that estimates SSB_{msy}. We begin by standardizing the S-R series by the areas of the nurseries used by each stock. This standardization allows comparison of productivity between stocks by removing the effects of differences in the size of the regions occupied by each stock.

Assume we have M stocks, and for each stock i we have n_i observations of the form (S_{ij}, R_{ij}), j=1....n_i. These observations are modelled as:

$$R_{ij} = \frac{\tilde{\alpha}_i S_{ij}}{1 + \left(\frac{S_{ij}(\sqrt{\tilde{\alpha}}_i - 1)}{SSB_{msy_i}} \right)} e^{\varepsilon_{ij}}$$

where $\tilde{\alpha}_i > 0$, $SSB_{msy_i} > 0$ and $\varepsilon_{ij} \sim N(0, \sigma_i^2)$. Note that as specified, error variance differs among stocks.

Taking the natural logarithms of both sides yields:

$$\log R_{ij} = \log(\tilde{\alpha}_i) + \log(S_{ij}) - \log(1 + \left(\frac{S_{ij}(\sqrt{\tilde{\alpha}}_i - 1)}{SSB_{msy_i}} \right) + \varepsilon_{ij} .$$

We define $\log \tilde{\alpha}_i = a + b_i$ and $\log SSB_{msy_i} = c + d_i$:

$$\log R_{ij} = a + b_i + \log(S_{ij}) - \log(1 + \left(\frac{S_{ij}(\sqrt{\exp(a + b_i)} - 1)}{\exp(c + d_i)} \right) + \varepsilon_{ij}$$

We fit this model under two assumptions about a, b_i, c and d_i. First we treat a, b_i, c and d_i as fixed effects. This is the equivalent to fitting to each S-R series individually, and is based on the unrealistic assumption that model parameters are not similar among populations of a taxonomic group. We also fit the model treating a and c as fixed, and b_i and d_i as random effects. Here, a and c are the means of $\log \tilde{\alpha}$ and $\log SSB_{msy}$ respectively, and b_i and d_i are the random deviates for each stock, such that:

$$\begin{pmatrix} bi \\ di \end{pmatrix} \overset{iid}{\sim} \mathrm{N}\left[\begin{pmatrix} 0 \\ 0 \end{pmatrix}, \begin{pmatrix} \sigma^2{}_b & 0 \\ 0 & \sigma^2{}_d \end{pmatrix} \right], i = 1, \ldots\ldots M .$$

Estimation and Inference:

The traditional mixed effects model is an alternative to the hierarchical Bayes approach that does not require the specification of a joint prior distribution for the fixed effects and variance components. Estimates are obtained using maximum likelihood, and are identical to empirical Bayes estimates, in that the priors are obtained from the data (often referred to as MLE priors). As such, they can be used as priors for Bayesian analyses of population dynamics for stocks where little data exists about the stock under investigation (Myers *et al*. accepted). Here, we obtain estimates for our models using the approximate maximum likelihood algorithm of Lindstrom and Bates (1990), using the S-

Plus nonlinear mixed effects library of Pinheiro and Bates (1999). These estimates are then interpreted as estimates of the productivity of the Gaspereau River alewife stock.

Data:

We used stock-recruitment time series from 5 alewife stocks in eastern North America (Table 4). $SPR_{F=0}$ is assumed constant across stocks, and is calculated using the data in Table 5. These data yield an estimate of $SPR_{F=0} = 0.325$. This means that one kg of age 3 recruits will produce 0.325 kg of spawners in its lifetime in the absence of anthropogenic mortality.

Parameter estimates for the individual and mixed effects models are presented in Table 6. Using individual models, very high estimates of $\tilde{\alpha}$ are obtained for some stocks, suggesting no relationship between spawner biomass and recruitment. However, when estimated using the mixed effects model, there is little variability in $\tilde{\alpha}$ between stocks, suggesting that $\tilde{\alpha}$ is relatively constant among alewife populations. Plots of the mixed effects spawner recruit relationship show that recruitment clearly declines at low spawner abundances (Figure 3). SSB_{eq} can be interpreted as the carrying capacity for an alewife stock in the absence of anthropogenic mortality. The between stock variability of SSB_{eq} (greater than an order of magnitude) is slightly larger than those of cod stocks in the ocean (Myers *et al*. in press). The "shrinkage" that occurs for the variability of estimates of $\tilde{\alpha}$ when estimated using the mixed effects model is less pronounced for SSB_{msy} (Figure 4).

Assuming a mean weight of 230 grams per fish, and using the fixed effect as an estimate of the productivity of the Gaspereau River alewife stock, the expected equilibrium spawning run size for this stock in the absence of fishing is around 2,807,000 fish. This is an estimate of the carrying capacity of the Gaspereau River watershed for alewife. Assuming all fish not captured complete the spawning run to Gaspereau Lake, SSB_{msy} occurs at 445,000 spawners, with a corresponding catch of 10,400 pails. If only 50% of the fish that ascend the White Rock ladder complete the spawning run to Gaspereau Lake, then the equilibrium White Rock count at SSB_{msy} is about 900,000 fish, with a corresponding catch of 6,872 pails.

3.3 Statistical Life History Modeling

The following model is currently under development, but under the constraints outlined below, can provide estimates of SSBmsy and SSBeq when fitted to the existing data for the Gaspereau River alewife stock. In our opinion, we are at the limit of data for this stock, but anticipate better model performance for alewife stocks where the data record is more complete.

Dynamical Model:

Let the subscript t index the year, s index the sex (m or f), a the age of the fish, and p index the number of times that fish has previously spawned

1. In any given year t, the number of eggs produced, E_t, may be expressed as:

$$E_t = \sum_{a,p} N_{t,\mathrm{f},a,p}(1-U_t)f_a$$

where: $N_{t,\mathrm{f},a,p}$ is the number of females of age a, that have spawned p times previously in the spawning run in year t, U_t is the exploitation rate in year t, and f_a is their age-specific fecundity.

2. The number of progeny that survive to reach the sea:

Given an instantaneous natural mortality rate within the spawning/nursery areas (M^{larval}), and a sex ratio(υ_s) the number of offspring of each sex that survive to migrate seaward in year t is:

$$O_{t,s} = E_t e^{-(M^{\mathrm{larval}})}\upsilon_s$$

Density dependent natural mortality within the spawning/nursery areas is thought to regulate *Alosa* population size. This is to say that the rate of juvenile natural mortality varies between years: i.e., $M_t^{\mathrm{larval}} = g(E_t)$, where g is a function of E_t that describes the nature of the density dependence. Hence:

$$O_{t,s} = E_t \mathrm{e}^{-(g(E_t))}\upsilon_s$$

3. Spawning run composition by age, sex and previous spawning history:

For fish that have not previously spawned, given a spawning run in year t, the number of fish within the run (downstream of the fishery) of sex s, age a, and that spawned p times previously is:

$$N_{t,s,a,0} = O_{t-a,s}e^{-T^{\mathrm{juv}}}m_{s,a}e^{-(M^{\mathrm{juv}}a)}$$

Here T^{juv} is the instantaneous rate of turbine mortality for juvenile fish and M^{juv} is the instantaneous natural mortality rate for immature fish at sea.

For fish that have spawned previously, given a spawning run in year t, the number of fish within the run (downstream of the fishery) of sex s, age a, and that spawned p times previously is:

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

4. We use spawner biomass (SSB) as a proxy for the number of eggs:

$$SSB_t = N_{t,a,\text{f},p} w_{t,a,\text{f},p} (1 - U_t)$$

5. Specifying that density dependent mortality is manifested through competition within a cohort yields a Beverton-Holt relationship for O_{t-a}, and the full dynamical model becomes:

$$N_{t,s,a,p} = \begin{cases} \dfrac{\alpha SSB_{t-a}}{\left(1 + SSB_{t-a} / K\right)} e^{-T^{\text{juv}}} \upsilon_s m_{s,a} e^{-(M^{\text{juv}} a)} & p = 0 \\ N_{t-p,s,a-p,0} e^{-\left(\sum_{k=t-p+1}^{t} F_k + T^{\text{adult}} p + \sum_{i=a-p}^{a} M_{s,a}^{\text{adult}}\right)} & p > 0 \end{cases}$$

This model can be adapted to specific stocks depending on the kinds of data that exist for that stock.

Adaptations for the Gaspereau River stock:

For the Gaspereau River alewife stock, the data consists of the catches for the years 1964 to 2000 (we use 1979 to 2000 in this model because of uncertainty in the process that resulted in large catches in the mid-1970's), counts at the White Rock ladder for the years 1982 to 1984, 1995, and 1997 - 2000, and the sex, age and spawning history composition for all years when counts were conducted except 1995. We do not have estimates of turbine mortality, which we drop from the model (its effects are explored in the next section), or juvenile natural mortality, which we assume is 0.4. We assume an adult instantaneous natural mortality of 0.6. We set up the model as follows:

1. Recruitment is defined as the number of fish in a cohort that survive to age 3. Recruitment in year *t* is modelled as a function of the spawner biomass in year *t*-3 assuming a Beverton-Holt spawner-recruit relationship. A logarithmic form of the model is used so that recruitment cannot go negative during model estimation:

$$\log R_t = \log(\alpha) + \log(SSB_{t-3}) - \log(1 + \left(\frac{SSB_t}{(\mathrm{R}_0 / \alpha)}\right) + \varepsilon_t$$

Here, R_0 is the mean asymptotic recruitment (the carrying capacity of the nursery areas scaled to survival at age 3), and ε_t is the recruitment deviate for year t around the spawner recruit relationship.

2. Recruitment is linked to the spawning run in the river through a sex ratio, a maturity schedule and at sea juvenile mortality:

$$N_{t,s,a,0} = R_{t-a+3} \upsilon_s m_{s,a} e^{-M^{\text{juv}}(a-3)}$$

We assume a sex ratio of 1:1.

3. We assume the fishery is non-selective. The composition of the catch in year t is given by:

$$C_{t,s,a,p} = N_{t,s,a,p} U_t$$

and the composition of the White Rock Count by:

$$WRC_{t,s,a,p} = N_{t,s,a,p}(1-U_t)$$

Here it is assumed that all fish not taken by the fishery ascend the White Rock fish ladder.

4. The count in one year is linked to the spawning run in the following year through adult natural survival:

$$N_{t+1,s,a+1,p+1} = WRC_{t,s,a,p} e^{-M^{adult}}$$

5. As mentioned, the catch is reported in pails. Assuming 127 fish/pail, the annual catch (C_t) is given by:

$$C_t = \left[\sum_{s=1}^{2} \sum_{a=1}^{\infty} \sum_{p=1}^{\infty} \left(N_{t,s,a,p} U_t \right) \right] / 127$$

and the spawning biomass (SSB_t) in kg:

$$SSB_t = \sum_{s=1}^{2} \sum_{a=1}^{\infty} \sum_{p=1}^{\infty} (N_{t,s,a,p}(1-U_t) w_{t,s,a,p})$$

As mentioned, under current management, only about half the alewives that ascend the White Rock ladder complete the migration to Gaspereau Lake. We therefore decrement the spawning biomass by 49%.

7. As in the previous section, SSBmsy is given by:

$$SSB_{msy} = K\sqrt{SPR_{F=0}\alpha} - K \quad \text{where } K = R_0 / \alpha \,.$$

We use the same $SPR_{F=0}$ estimate as in the previous section.

8. We fit the model to the data by minimizing an objective function value that is the weighted sum of the non-constant portions of the negative log-likelihoods of the catches, counts and sex/age/previous spawning compositions. Assuming lognormal errors for the catches and the White Rock count, the non-constant proportions of the negative log-likelihoods are:

$$\lambda_{catch} = \sum_t (\ln C_t^{obs} - \ln C_t^{pred})^2$$

$$\lambda_{count} = \sum_t (\ln WRC_t^{obs} - \ln WRC_t^{pred})^2$$

Assuming multinomial errors for the sex/age/previous spawning composition of the spawning run, the non-constant proportion of the negative log-likelihood is:

$$\lambda_{composition} = -\sum_t \sum_s \sum_a \sum_p n_{t,s,a,p} \ln p_{t,s,a,p}$$

The objective function value that is minimized is:

$$O.B.V. = \lambda_1 \lambda_{composition} + \lambda_2 \lambda_{catch} + \lambda_3 \lambda_{count}$$

where the λ's are the weighting factors that keep any one part of the objective function from dominating the fit.

The Gaspereau River alewife dataset has a period of 14 years where the only data is the catch. Prior to this period, we have three years of data where we have escapement counts and the sex/age/previous spawning composition of the run, and four years at the end of this period with the same types of data. We initially set up the model to estimate an exploitation rate in each year, alpha, natural mortality and asymptotic recruitment (constant across years), and a recruitment deviate for each year. While ADModel Builder provided parameter estimates that appeared reasonable, as a result of the limited data, model parameters are confounded resulting in a Hessian matrix that was not positive definite (standard errors could not be calculated for the parameter estimates). For the years when fish ascending the White Rock ladder is known, we have good estimates of the exploitation rate. We therefore chose to treat the exploitation rate as known, using the calculated exploitation rate when available, and the mean of the calculated exploitation rate for the years (1982 -1984, 1997 and 1998) as an estimate of the exploitation rate for other years (0.725). These values were fixed in the model. We set up the model to

estimate the mean asymptotic recruitment, R_0, and a recruitment deviate for each year. K and SSB_{msy} are calculated from α and R_0. We attempted to estimate α within the model as well, but were unable to do so. We therefore set $\alpha = 100$ in the model, estimated R_0, and then calculated K and SSB_{msy} using $\alpha = 60.7$ (from the hierarchical model).
Parameter estimates and their standard errors are shown in Table 7. The fit of the model to the numbers at age data appears reasonable (Figures 5-6). As weighted, the model tracks the count very closely, and fits the catch reasonably well except during the 1984 to 1988 time period (Figure 7). There is considerable scatter in the spawner-recruit series (Figure 8). Assuming a mean weight 230g/fish, the estimated SSB_{msy} implies that MSY occurs with an equilibrium spawner abundance of 400,000 alewives. Again, if only 50% of the fish that ascend the White Rock ladder complete the spawning run to Gaspereau Lake, the equilibrium White Rock count at SSB_{msy} is around 800,000 fish.

3.3 Effects of Turbine Mortality

Under the current water management strategies in the Gaspereau River watershed, alewives are diverted from passing through 4 of the 5 hydroelectric stations. The models presented in the preceding sections do not include the effects of mortality resulting from downstream passage at the White Rock generating station (referred to as "passage mortality" in the following discussion, and assumed to include the combined effects of turbine mortality and fish bypass effectiveness). Passage mortality at White Rock has not been studied, but could potentially have a large effect on alewife production in the Gaspereau watershed. We incorporate the effects of passage mortality by adding adult and juvenile mortality to the SSB_{msy} models previously presented. We illustrate the potential impacts using the parameter estimates from the statistical life history model.

Juvenile mortality is included in the model by reducing α and R_0 by a factor of $1-T_{juv}$, where T_{juv} is the proportion of fish that do not survive passage at the White Rock. Juvenile passage mortality has the effect of reducing both SSB_{msy} and the catch at MSY in direct proportion to the level of mortality (Figure 9). Adult passage mortality can be incorporated in the model by reducing the survival of post-spawning adults in the SPR calculation. The effect of adult passage mortality is less severe than juvenile mortality (Figure 9), because both the fishery and reproduction occur before adult passage mortality. Here, the fishery is sustainable even in the presence of 100% adult passage mortality.

Given high levels of passage mortality, optimization of the fishery in terms of MSY is probably not a precautionary management strategy. Rather, optimization of the production of alewives could better ensure the survival of the stock. Under this scenario, spawner abundance would be kept high, and the catch would decline as a function of passage mortality. While not modelled as part of this report, there would exist some level of passage mortality (less than 100%) for which the allowable catch would be zero.

4. DISCUSSION

The Gaspereau River alewife stock exhibits characteristics of a heavily impacted stock. In 2000, only 11.1% of males, and 7.4% of females in this run had previously spawned. This percentage can be over 50% in un-impacted stocks. As a result, the population relies primarily on only 2 year classes, instead of 6 or more year classes in an un-impacted stock. The exploitation rates for 1999 and 2000 are near 90%. While the biological limits of the Gaspereau River alewife stock are currently unknown, Crecco and Gibson (1990) report annual fishing mortality rates at the maximum sustainable yield (u_{msy}) and at stock collapse (u_{coll}) for four North American alewife stocks of 64.5% and 77.0% respectively, well below the exploitation rates reported herein. In this report we have estimated the spawning escapement that produces maximum sustainable yield using two methods. While neither model produces precise estimates, the analyses are nearly independent of each other, and produce similar results. These suggest that 400,000 to 450,000 spawners are required to produce MSY. Currently, only about 10 to 20 % of these numbers reach Gaspereau Lake to spawn.

While neither model currently produces precise estimates of SSB_{msy}, we anticipate better performance from both models as model development proceeds and with more data. Both models are currently in the developmental stage. Five datasets is a relatively small number for a mixed effects model, and we anticipate that as more data sets are added, more precise estimates of SSB_{msy} may be obtained. However, the high variability in productivity of these stocks is similar to that reported for other species such as Atlantic cod (Myers *et al*. in press). If this variability is inherent within fish stocks, it may limit the usefulness of estimates SSB_{msy} from mixed models as predictors of the productivity of stocks without stock specific data. Alternatively, other model formulations may provide better estimates. In the current formulation, alewife production is assumed to be a linear function of the size of the nursery area. If large lakes or reservoirs are less productive, or not all of their area is utilized, a logarithmic relationship may be more appropriate. Additionally, productivity might also be expected to vary with latitude or water temperature. As more datasets are added to the model, these types of relationships can be explored, and should increase the utility of the model.

We believe the life history modelling presented in this report is stretching the limits of what can currently be done with the Gaspereau River alewife data. While the model produces parameter estimates that appear reasonable for alewife, without constraints (such as treating fishing mortality as known) we were unable to produce estimates of the uncertainty associated with these estimates. We expect the model to produce better results when using datasets that are more complete. If data collections continue on the Gaspereau River, we expect this approach to yield good estimates of the productivity of this system. As it is, treating the exploitation rate as known is probably not an unreasonable assumption. For years when we have counts of the spawning escapement, the exploitation rate can be calculated directly. With the exception of water management in 1999 and 2000, we are not aware of any management change during the time period that was modelled that would cause a significant change in the mean exploitation rate for this stock. As programmed, the model treats the maturity schedule as constant across years. This is not a biologically reasonable assumption, and spawning run size is influenced by changes in the maturity schedule between years. As presented, the model

had difficulty fitting around the low catch in 1988. We believe this low catch may be the result of such a change. Model development should proceed using a better dataset to explore the effects of these types of phenomena on the size of the spawning run and management. Additionally, other sources of anthropogenic mortality, such as turbine mortality, are not currently included in the model, but could substantially impact the productivity of the stock. Finally, components to evaluate risk and uncertainty within a Bayesian context should be added to the model, although these will require consensus on management targets. We believe that with the appropriate modifications, this modelling approach can provide an excellent management tool for this stock.

From a conservation perspective, water management in the Gaspereau River and management of the alewife fishery cannot be uncoupled. During 1999 and 2000, water levels in the Gaspereau River have been maintained at a lower level during May to conserve water for Atlantic salmon. At the lower water levels, less cross-sectional area of the river is available for fish to avoid the fishers' nets, thus increasing the efficiency of their gear. We believe this decision has contributed to the high exploitation rates during these years. It follows that consultation between the fishers, NSPI and DFO, well prior to the start of the fishing season is necessary to ensure that trap sites are appropriately designed for an anticipated water level (and aren't in violation of DFO regulations).

During 1997 to 1999, when fish were counted entering Gaspereau Lake, post-spawning adults were observed moving downstream at White Rock before post-spawning adults were observed leaving Gaspereau Lake. Additionally, alewives continued to ascend the ladder at White Rock after fish have stopped moving into Gaspereau Lake. We do not believe that reproduction downstream of Gaspereau Lake contributes significantly to the productivity of this stock. Under current management, fishers may start the season when fish first enter the river and may continue to fish (except weekends and at night) until the end of May. This strategy selects against the older, larger fish that are present earlier in the run. Delaying the start of the fishery to allow a greater portion of the early part of the run the opportunity to spawn, and additional closures early in the season, could substantially increase spawning escapement. In years when the run is large, the season could be extended to allow fishing on the tail of the run. If the counts at White Rock are continued during the next few years, the opportunity exists for in-season tuning of the fishing effort in the Gaspereau River to ensure adequate spawning escapement during these years. Such a program would provide an opportunity to determine a level of fishing effort that would provide adequate spawning escapement in most years. Such a project would require consultation and collaboration on the part of the fishers, NSPI and DFO.

Perhaps the most restrictive water management strategy on the Gaspereau River, is the closure of the control gate at Forest Home, which occurs shortly after alewives first enter Gaspereau Lake in May. The gate is currently kept closed until mid-August, when young-of-the-year alewives are large enough that the Trout River Pond diversion screen is effective. This strategy allows alewives to bypass 4 of the 5 generating stations in the watershed. However, because the largest storage basins in the watershed are upstream of this gate, this strategy places limits on the amount of water available for other purposes, such as Atlantic salmon conservation. From the perspective of alewife, the strategy

provides protection for eggs and larvae (adults could be excluded using the diversion screen), which are pre-compensation life stages that provide less benefit to the stock than the protection of post-compensation life stages. Given adequate spawner abundance, this gate could potentially be kept open further into May or June (with the screen in place to protect adults), allowing greater flexibility in water management during the summer. Prior to the adoption of such a plan, acceptable levels of egg and larval loss for a given spawner abundance should be modeled, and the rate of egg and larval transport monitored at Forest Home to determine the actual rate of loss. Given the caveat that spawner abundance needs to be adequate before relaxing the restrictions on the Forest Home gate operation, this example illustrates how water management and the alewife catch are directly linked.

Fish passage mortality at the White Rock Generating is not known, but is an important variable for the determination of both the limits of fishing and the importance of effective bypass facilities at White Rock. The deterministic, equilibrium models presented in this report show that if managing for maximum sustainable yield, juvenile passage mortality decreases both the catch and spawning escapement it direct proportion to the level of juvenile mortality. Because adult passage mortality occurs after reproduction, the fishery is sustainable even at high levels of adult passage mortality, albeit at lower harvest levels. It follows that passage mortality of adults and juveniles needs to be quantified before the harvest or spawning escapement targets can be established.

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Table 1. Summary of Gaspereau River alewife catches between 1964 and 2000.

Statistic	Catch (pails)
Mean	7,120
Minimum	1,099
Maximum	20,744
Median	5,600

Table 2. Summary of alewife counts at the White Rock fish ladder, estimated stock size, and the annual catch and exploitation rates of the alewife fishery.

Year	Alewife Count	Catch (number of fish)	Stock Size	Exploitation Rate (%)
2000	98,883	754,585**	853,468	88.4
1999	81,326	698,600**	770,926	89.4
1998	171,639	372,400***	544,039	68.5
1997	95,433	611,520*	706,953	86.5
1995	126,933 (partial)	954,960*	>1,081,893	<88.3
1984	111,100	212,966**	324,066	69.9
1983	114,800	150,408**	265,208	56.7
1982	50,400	254,068**	304,468	80.9
1970	60,527	480,000*	540,527	88.9

* assuming 120 alewives/pail
** number of alewives/pail adjusted from * by mean weight/alewife
*** assuming 133 alewives/pail

Table 3. Summary of Gaspereau River alewife stock characteristics. Numbers in brackets are standard deviations.

Characteristic	Sex	Year 1982	1983	1984	1997	1998	1999	2000
Mean Fork Length (mm)	Males	268.7 (10.6)	252.9 (15.0)	263.0 (12.0)	255.5 (10.5)	247.6 (14.7)	243.6 (10.4)	251.6 (12.2)
	Females	279.4 (11.6)	268.5 (17.8)	272.8 (11.7)	265.0 (14.1)	257.0 (16.1)	252.3 (11.2)	263.0 (11.6)
Maximum Fork Length (mm)	Males				287	299	278	285
	Females				315	302	286	311
Mean Weight (g)	Males	272.1 (34.5)	232.4 (48.6)	254.2 (38.9)	221.4 (29.8)	212.3 (42.5)	194.2 (27.6)	227.0 (34.0)
	Females	315.7 (48.5)	290.4 (67.4)	288.0 (44.8)	253.7 (40.3)	244.6 (50.8)	221.8 (32.1)	265.0 (35.0)
Mean Age (y)	Males	5.0 (0.49)	4.5 (0.69)	4.8 (0.52)	4.29 (0.59)	4.36 (0.60)	4.36 (0.54)	4.63 (0.56)
	Females	4.63 (0.56)	4.9 (0.83)	5.0 (0.46)	4.50 (0.76)	4.41 (0.58)	4.42 (0.49)	4.81 (0.58)
Maximum Age (y)	Males	7	7	7	6	7	6	6
	Females	7	7	7	7	6	5	6
Mean Age at First Spawning (y)	Males	4.89	4.36	4.63	4.11 (0.39)	4.10 (0.39)	4.18 (0.45)	4.53 (0.55)
	Females	4.89	4.61	4.82	4.18 (0.42)	4.19 (0.42)	4.29 (0.48)	4.71 (0.580
Repeat Spawners (%)	Males	8.2	12.1	15.4	15.1	32.7	15.2	11.1
	Females	12.2	22.0	11.5	24.8	23.5	11.5	7.4

Table 4. Stock - recruitment time series used for the mixed effects modelling.

River	Spawning Area (km^2)	Years Available	Data Source
Annaquatucket River RI	1.01	1945 - 1989	Crecco and Gibson 1990
Long Pond ME	3.86	1950 -1955	Havey 1961
Damariscotta River ME	18.06	1977 -1984	Walton 1986
Lamprey River NH	0.1	1972 - 1985	Crecco and Gibson 1990
Saint John River NB	87.3	1968 - 1982	Jessop 1990
Gaspereau River NS	22.9[a]	1981 - 2000	

a. sum of the areas of Gaspereau, Two Mile and Four Mile Lakes

Table 5. Values used for calculation of $SPR_{F=0}$. The weights are estimated from a LVB model fit to the Gaspereau River data (1997 - 2000). Maturity probabilities are the estimates from the catch-at-age/life history model in the next section of this report.

	Age (yr)						
	3	4	5	6	7	8	9+
Weight (g)	193	219	264	304	330	347	356
Maturity Probability	0.01	0.40	0.98	1	1	1	1
M_{juv}	0.4	0.4	0.4	0.4	-	-	-
M_{adult}	0.6	0.6	0.6	0.6	0.6	0.6	0.6

Table 6. Estimates of lifetime maximum reproductive rates ($\tilde{\alpha}$), spawning biomass at equilibrium in the absence of anthropogenic mortality (SSB_{eq}) and spawning biomass at maximum sustainable yield (SSBmsy) for 5 alewife stocks. Estimates are obtained by fitting a Beverton Holt stock-recruitment model to each stock individually, and by fitting the model to each stock simultaneously using a mixed effects model.

	individual esimates			mixed effects estimates		
River	$\tilde{\alpha}$	SSB_{eq} (t/km^2)	SSB_{msy} (t/km^2)	$\tilde{\alpha}$	SSB_{eq} (t/km^2)	SSB_{msy} (t/km^2)
Annaquatucket River RI	271.8	69.33	3.9	20.1	57.9	10.1
Long Pond ME	>10,000	2.17	<0.01	20.1	3.56	0.6
Damariscotta River ME	17.0	53.3	9.4	20.1	35.8	6.3
Lamprey River NH	18.23	194.5	34.8	20.1	169.0	31.2
Saint John River NB	76.5	6.8	0.68	20.1	8.0	1.4
mean or fixed effect				20.1	28.2	4.47
95% confidence interval				15.1 to 26.2	6.84 to 166.4	1.23 to 16.23

Table 7. Parameter estimates for the Gaspereau River alewife stock obtained from the statistical life history model.

Year	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	1.5
1998	0.12	5.9
1999	0.32	1.5
2000	-0.81	0.59
R_0	1,647,800 fish	602,330
SSB_{msy}	91,939 kg	33,607

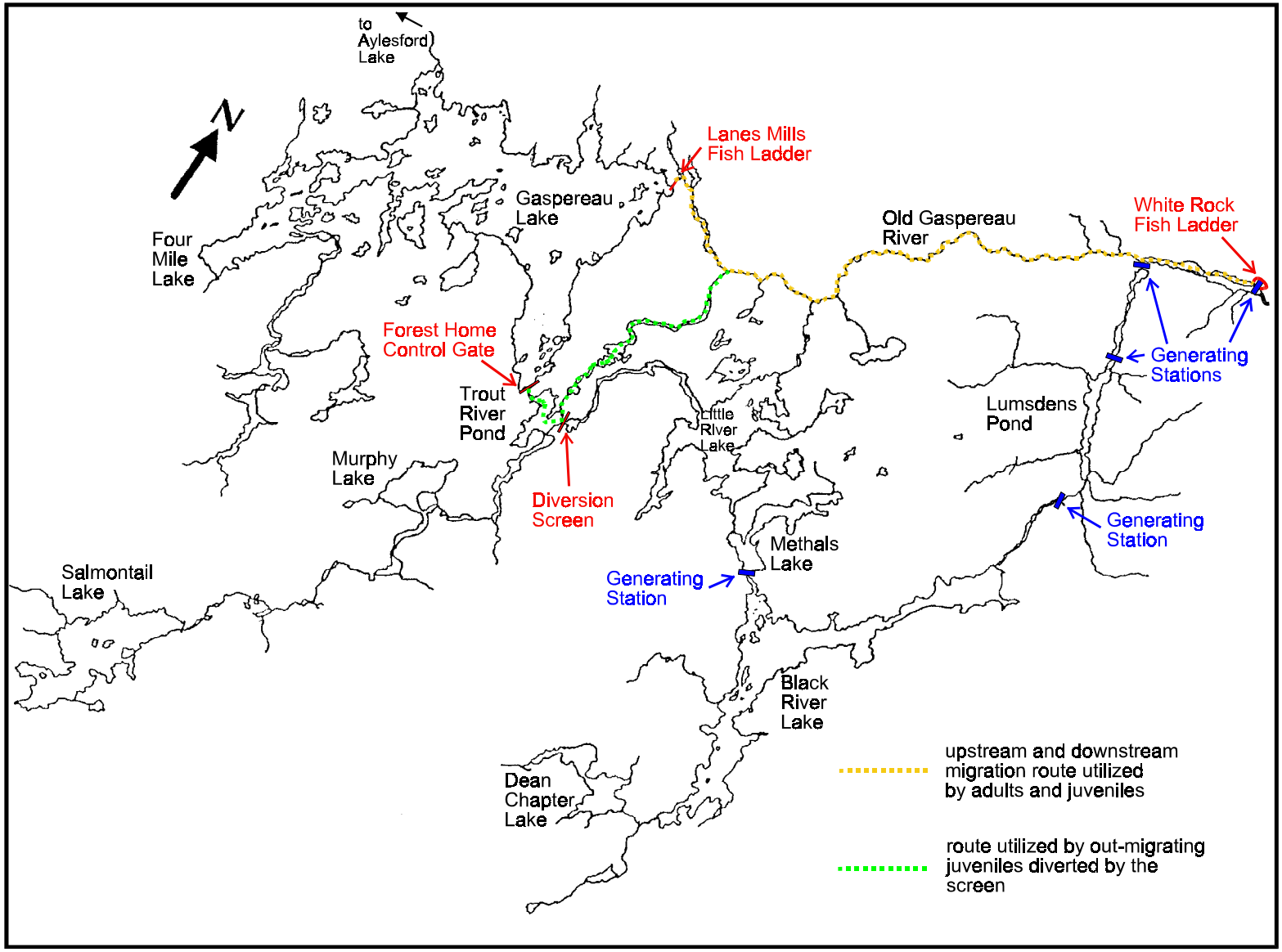

Figure 1. Partial map of the Gaspereau River watershed showing migration routes used by alewives.

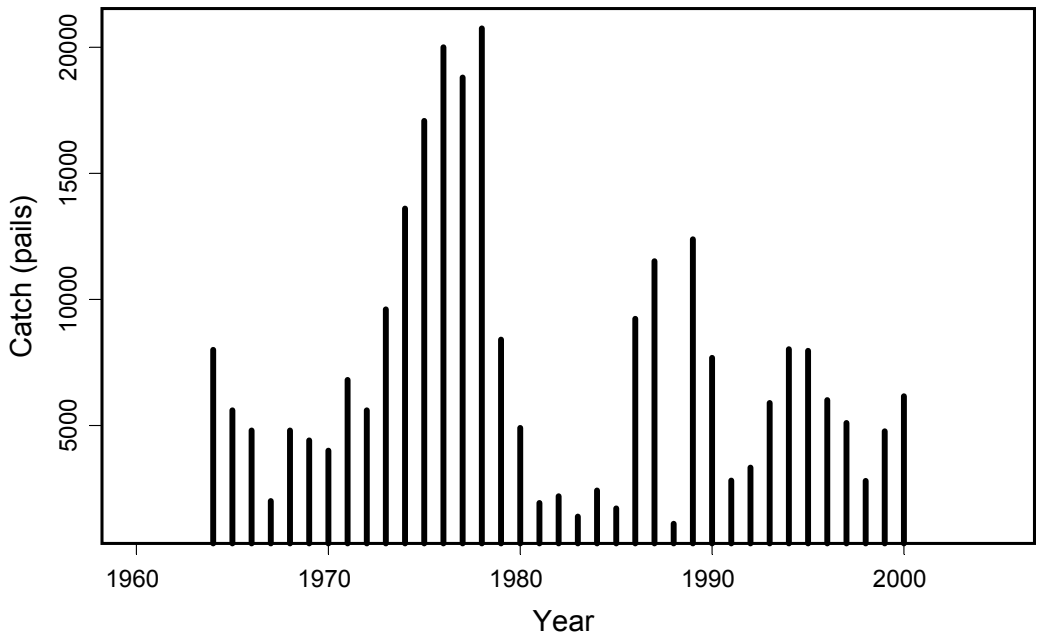

Figure 2. The Gaspereau River alewife catch from 1964 to 2000. One pail contains about 127 fish.

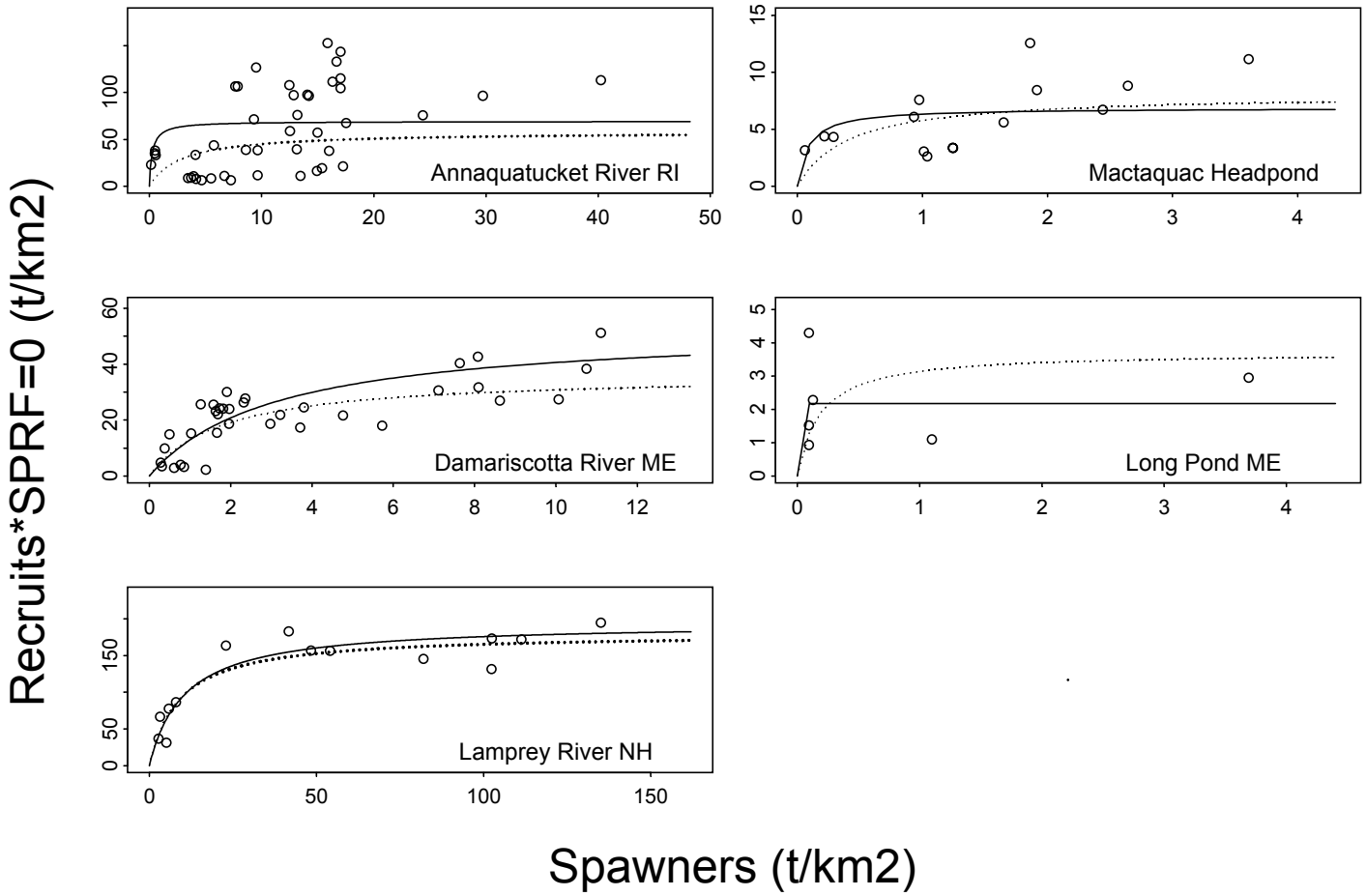

Figure 3. Recruitment as a function of spawner biomass for the 5 stocks used in the hierarchical model. The solid line is the Beverton Holt model fitted to each stock individually, and the dotted line is the fit produced with the mixed effects model. Recruitment and spawning biomass are standardized by the area of the nurseries in the watershed. Recruitment is rescaled by the number of spawners a recruit would produce throughout its lifetime in the absence of anthropogenic mortality.

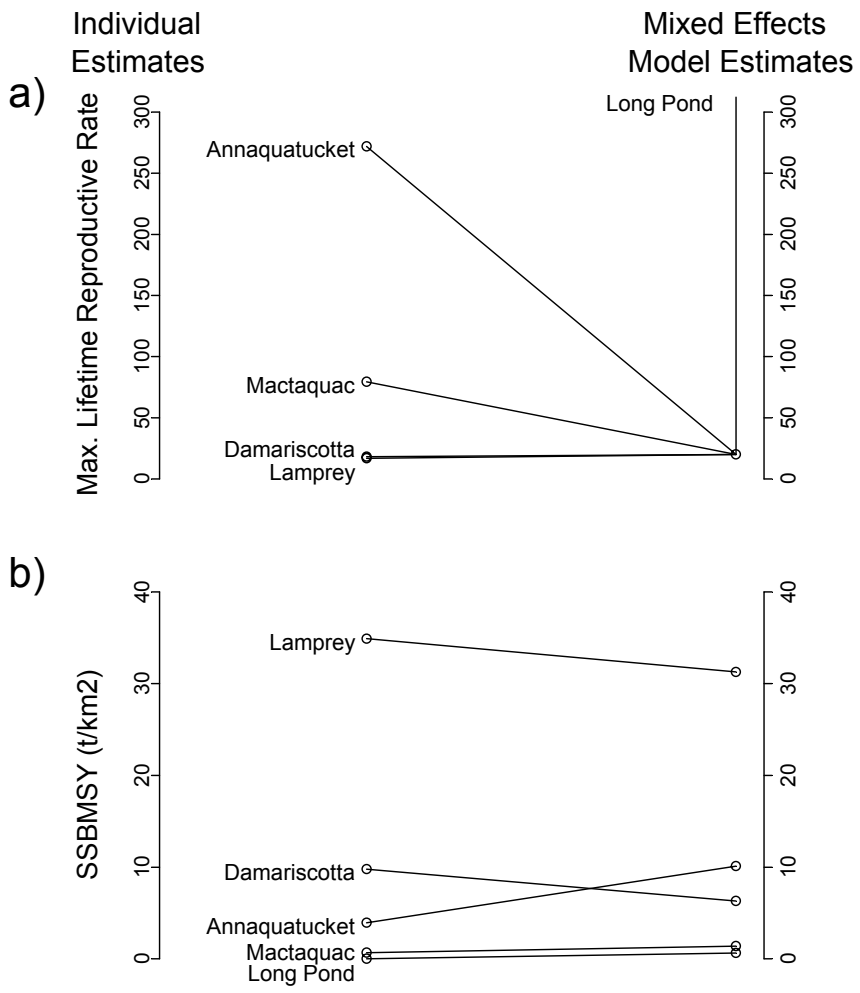

Figure 4. A comparison of the estimates of the maximum lifetime reproductive rate (top) and spawning biomass at maximum sustainable yield (bottom) obtained fitting Beverton Holt stock recruitment models to each stock individually and using the mixed effects model. The estimate of the maximum lifetime reproductive rate for Long Pond is extremely high and is outside the area of the plot.

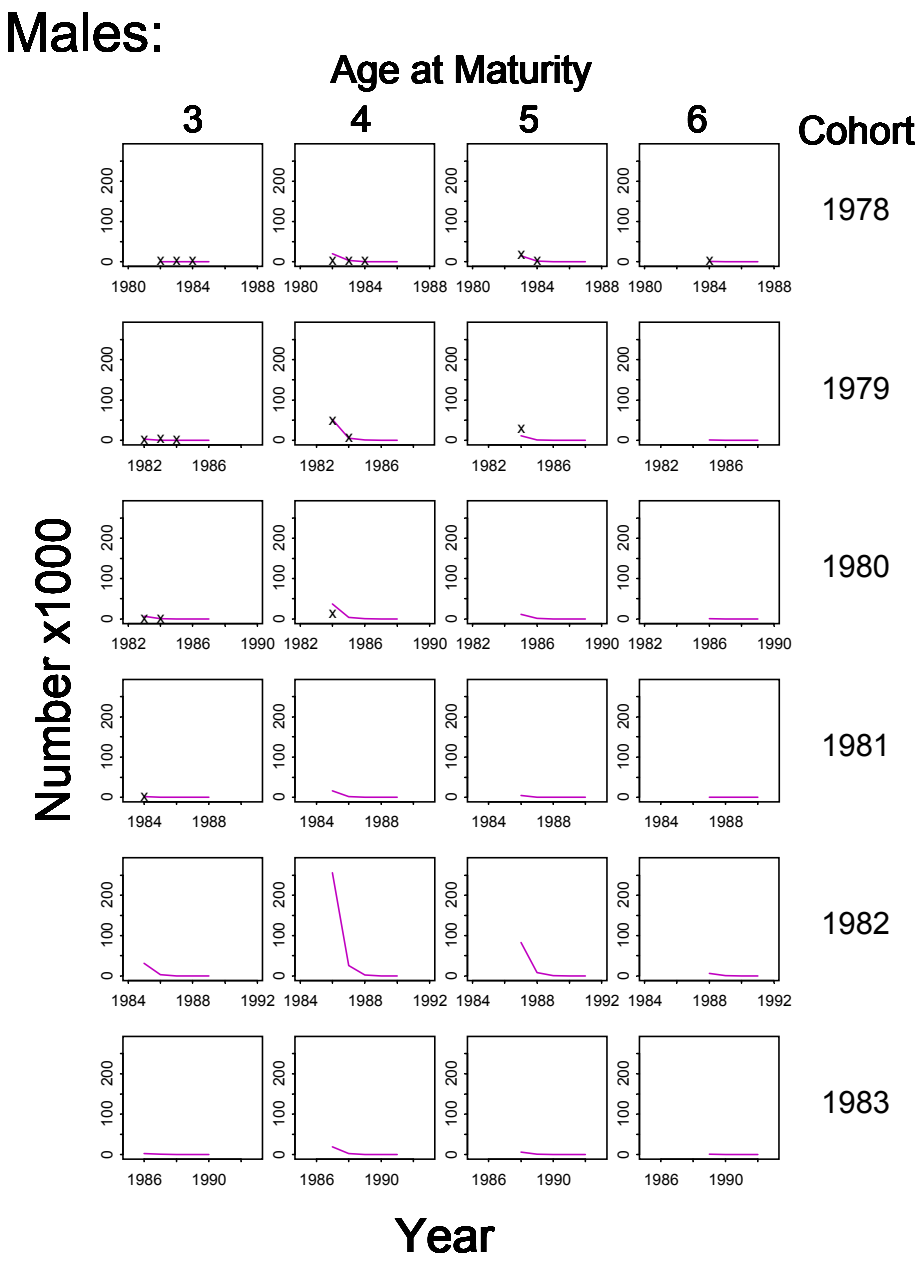

Figure 5. Predicted (line) and observed (x) spawning escapement of male alewives by cohort and age at maturity for the Gaspereau River alewife stock. Output is from the life history model.

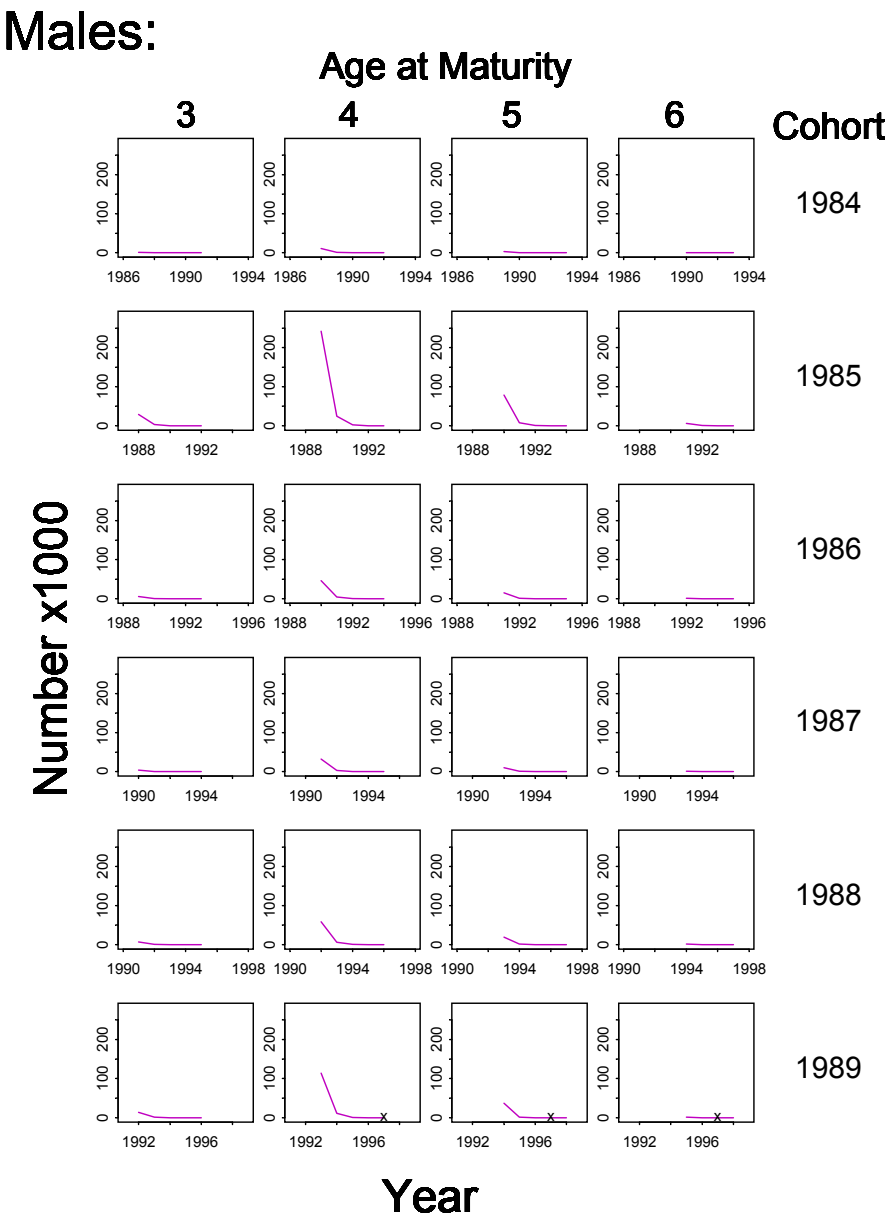

Figure 5 (con't). Predicted (line) and observed (x) spawning escapement of male alewives by cohort and age at maturity for the Gaspereau River alewife stock. Output is from the life history model.

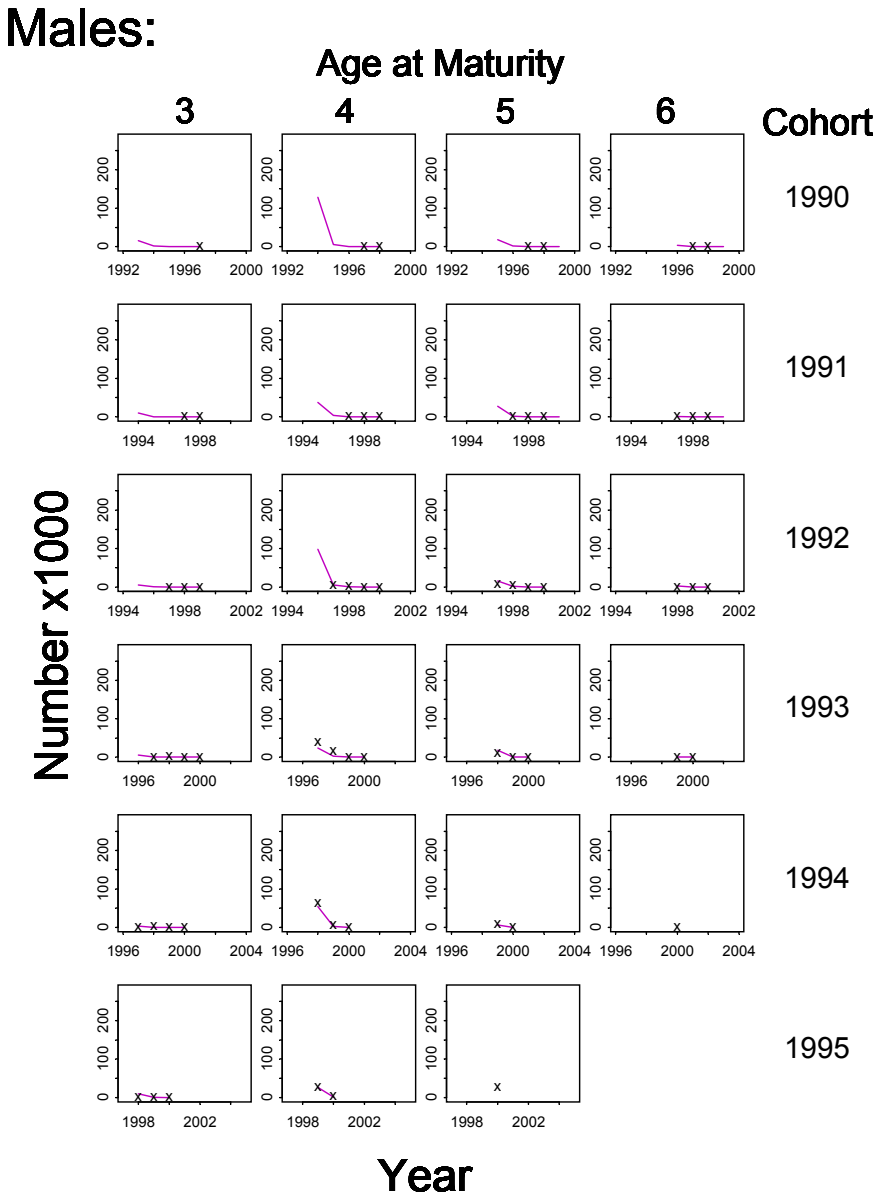

Figure 5 (con't). Predicted (line) and observed (x) spawning escapement of male alewives by cohort and age at maturity for the Gaspereau River alewife stock. Output is from the life history model.

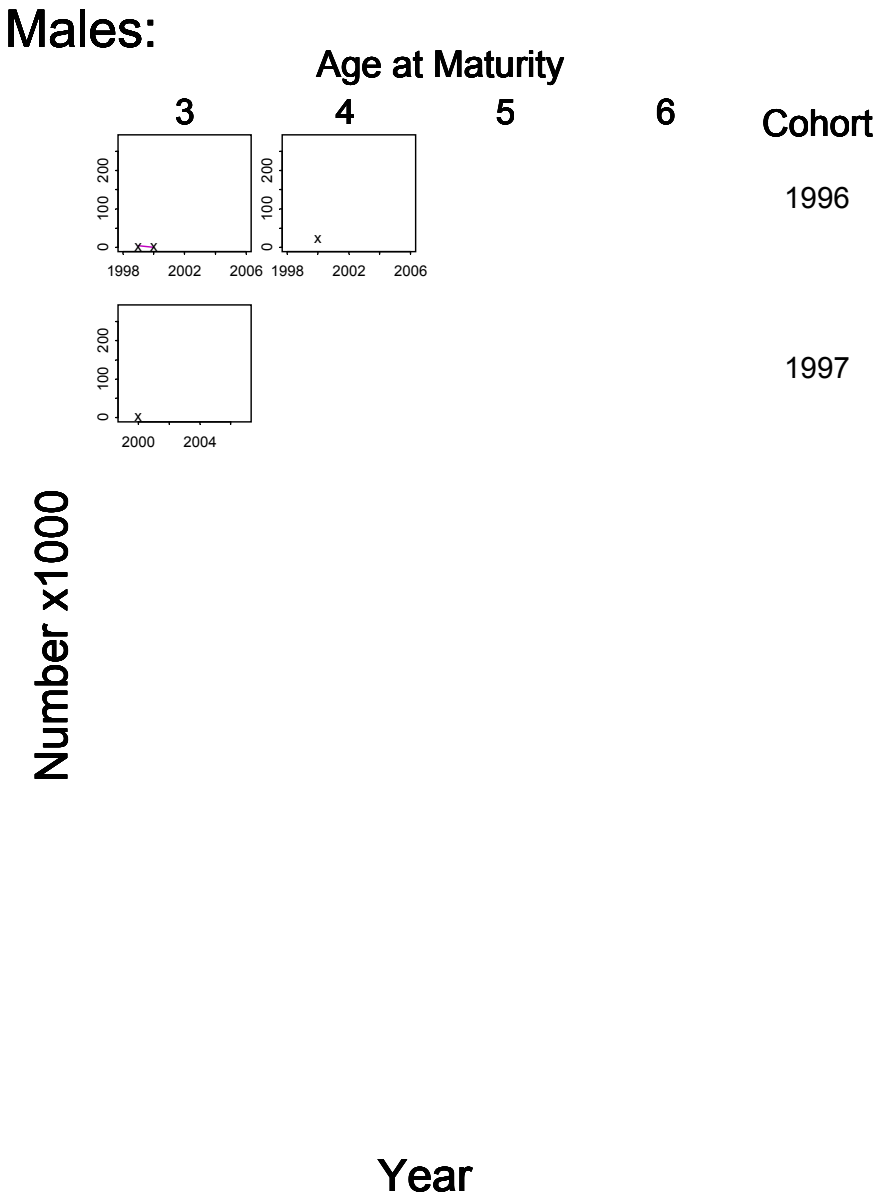

Figure 5 (con't). Predicted (line) and observed (x) spawning escapement of male alewives by cohort and age at maturity for the Gaspereau River alewife stock. Output is from the life history model.

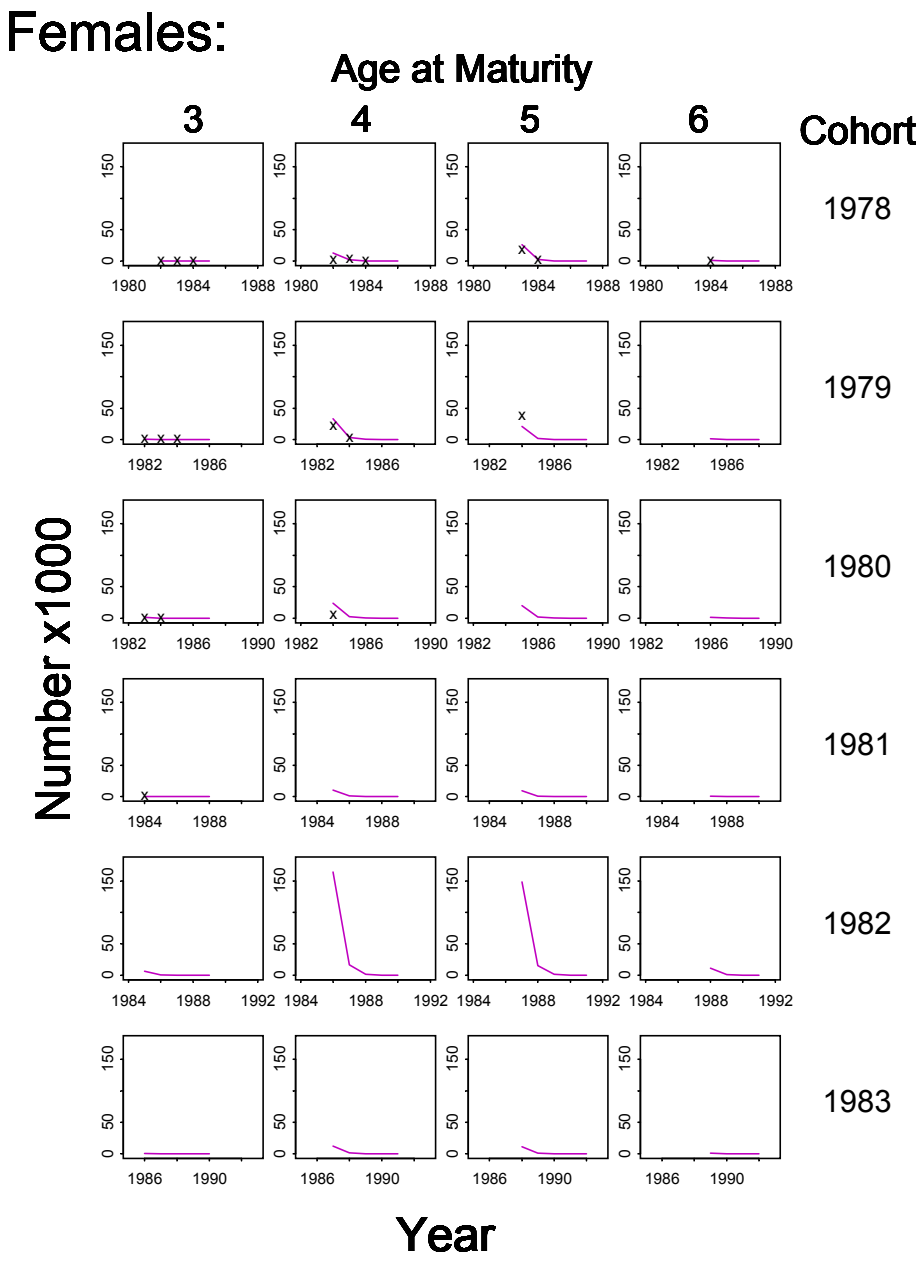

Figure 6. Predicted (line) and observed (x) spawning escapement of female alewives by cohort and age at maturity for the Gaspereau River alewife stock. Output is from the life history model.

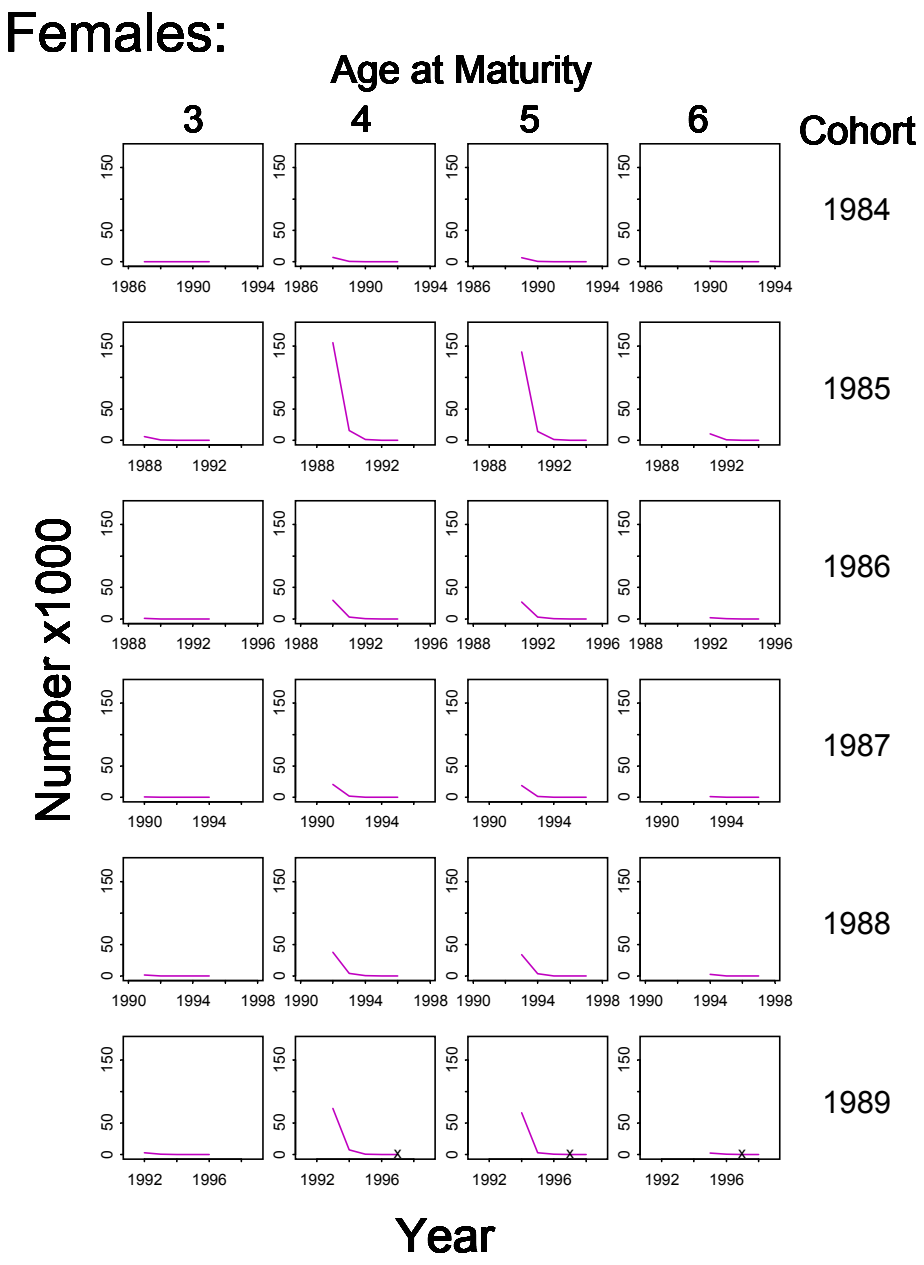

Figure 6 (con't). Predicted (line) and observed (x) spawning escapement of female alewives by cohort and age at maturity for the Gaspereau River alewife stock. Output is from the life history model.

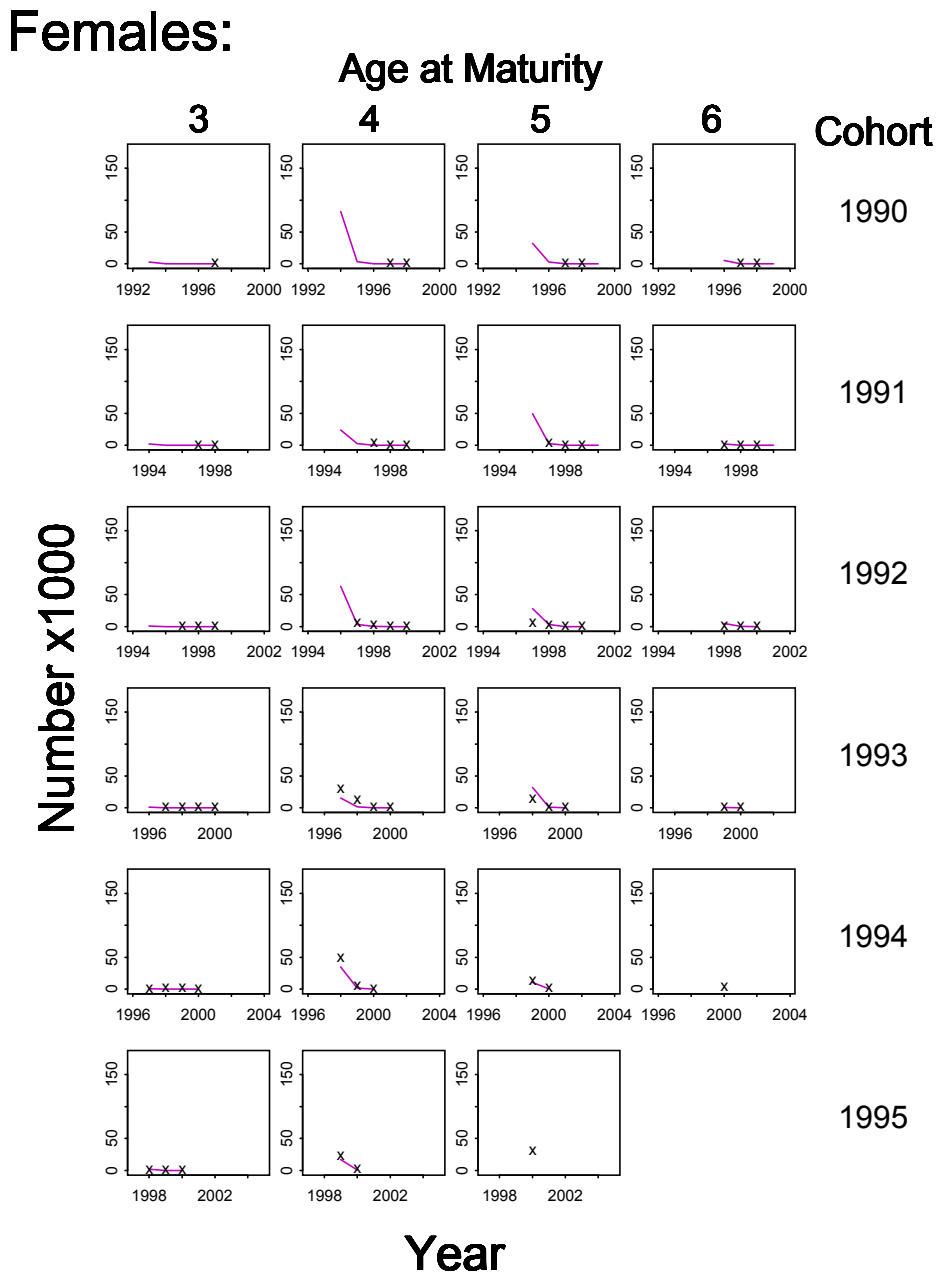

Figure 6 (con't). Predicted (line) and observed (x) spawning escapement of female alewives by cohort and age at maturity for the Gaspereau River alewife stock. Output is from the life history model.

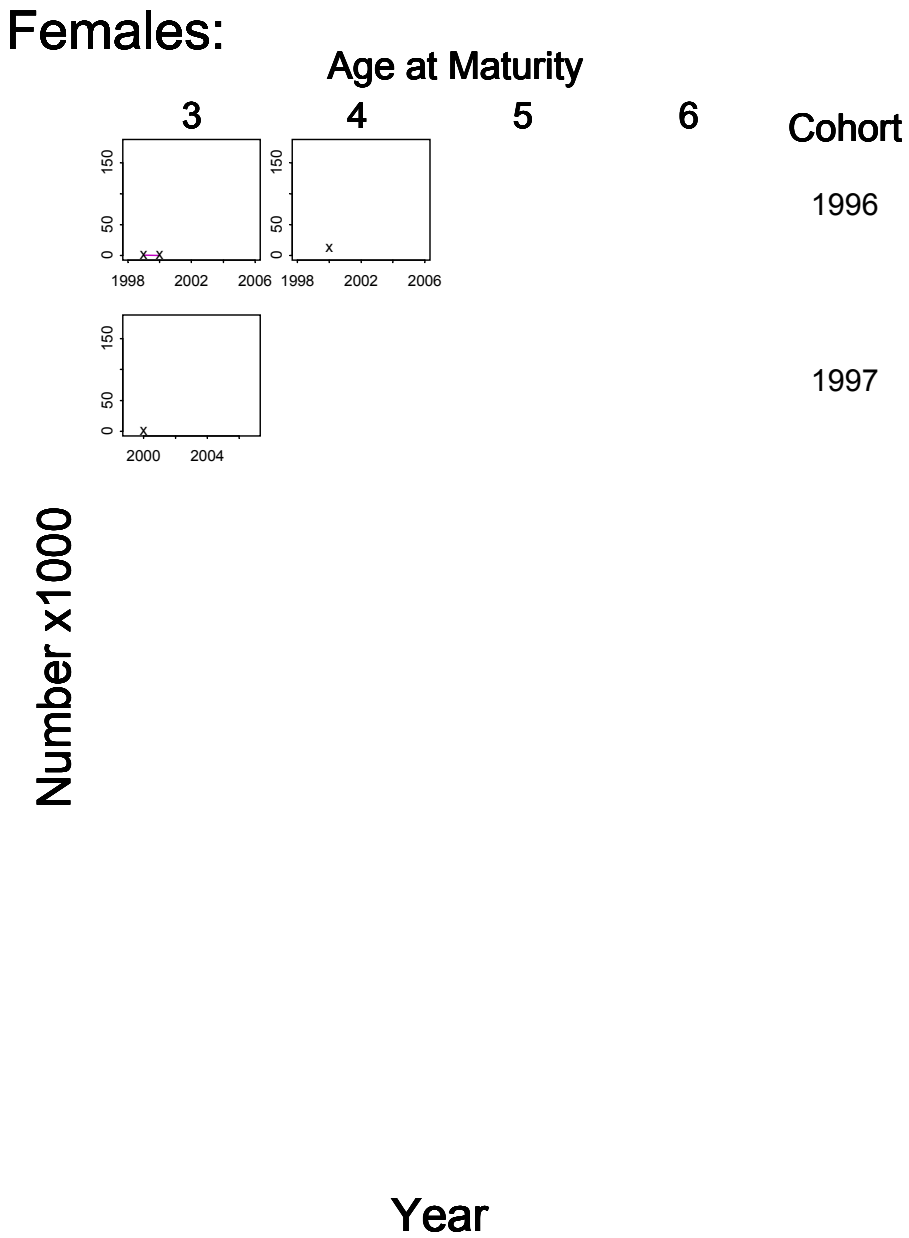

Figure 6 (con't). Predicted (line) and observed (x) spawning escapement of female alewives by cohort and age at maturity for the Gaspereau River alewife stock. Output is from the life history model.

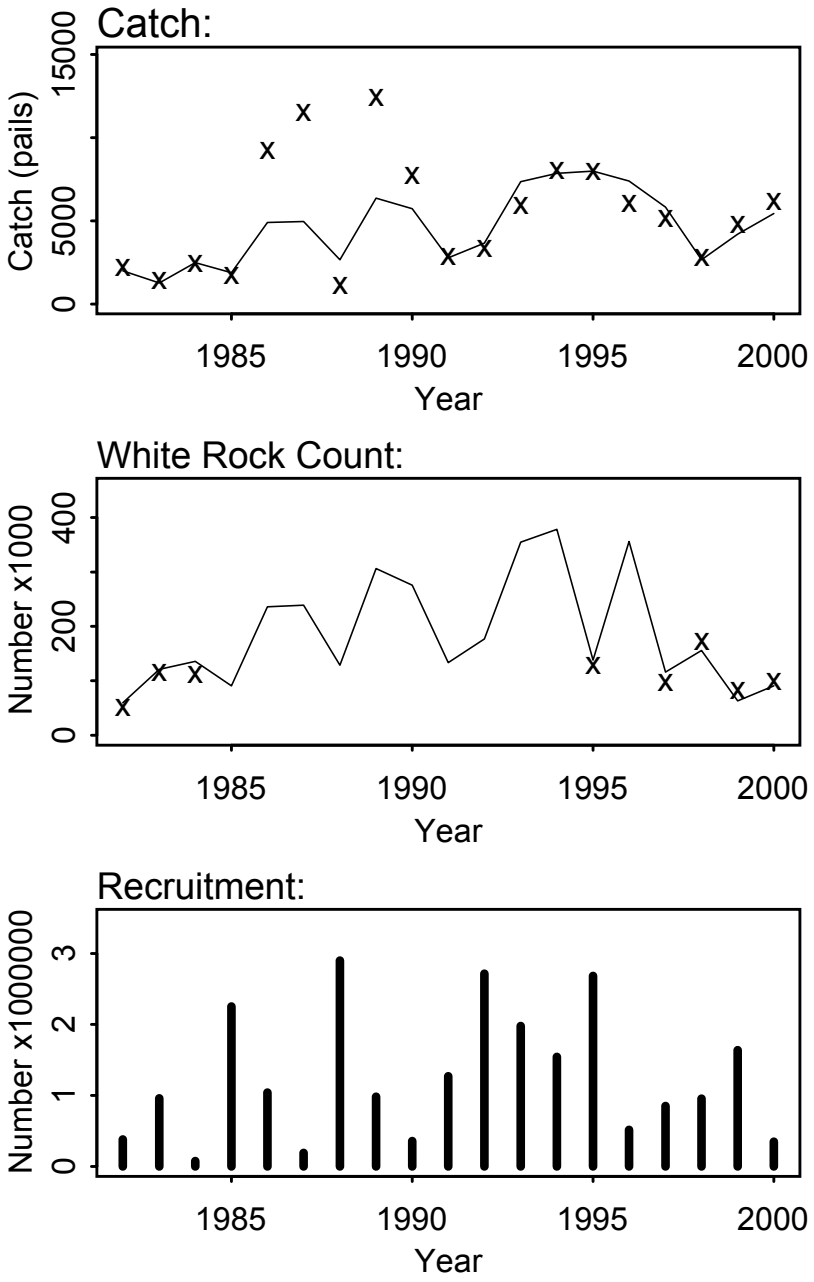

Figure 7. Predicted (line) and observed (x) catches (top), counts (middle) and predicted number of age 3 recruits (bottom) for the Gaspereau River alewife stock. Output is from the life history model.

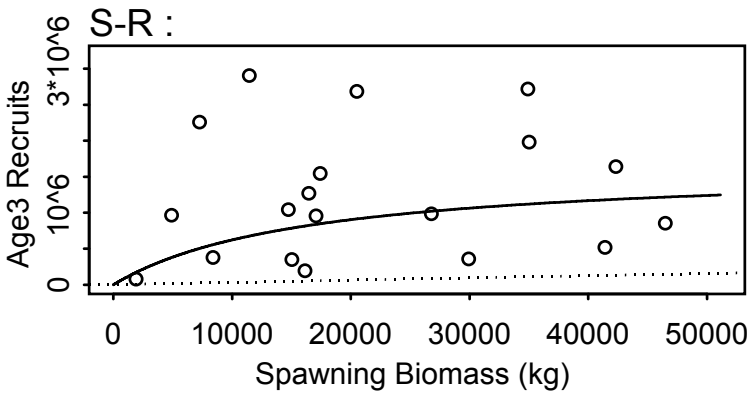

Figure 8. Beverton-Holt spawner recruitment model for the Gaspereau River alewife stock. Data points are predicted using the life history model. The dotted line is the replacement line.

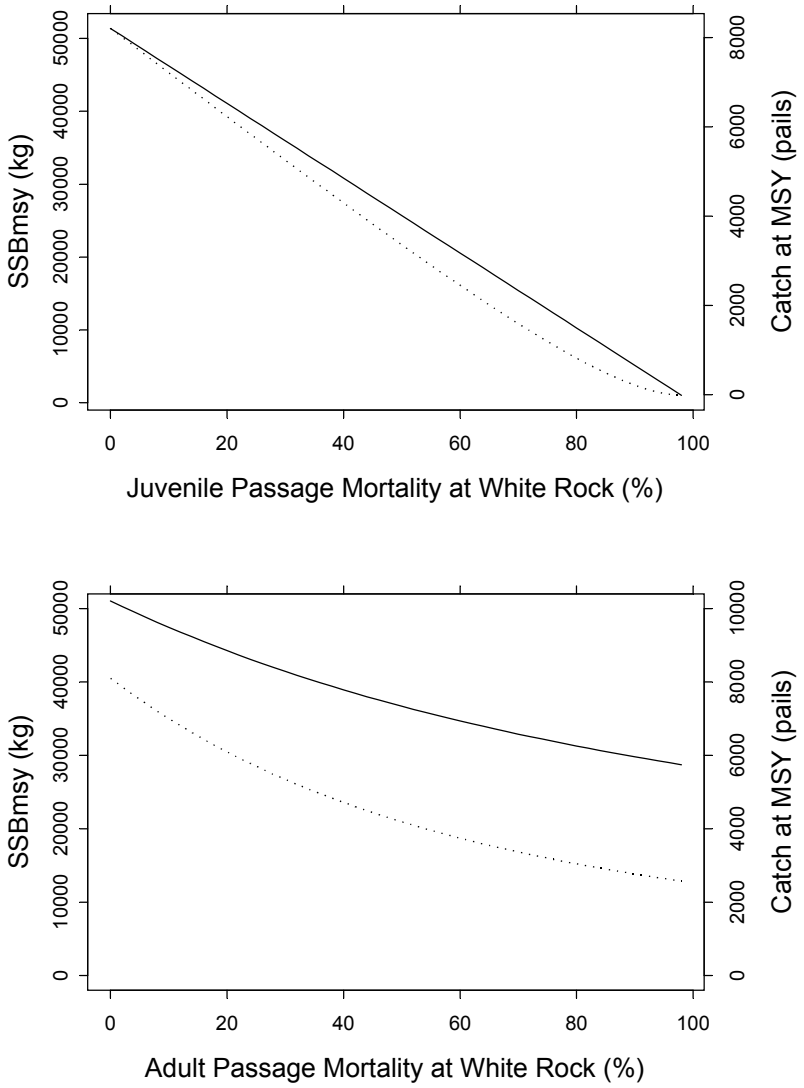

Figure 9. Relationship between spawning biomass (solid line) and catch (dotted line), and passage mortality at the White Rock dam. Model parameters are taken from the life history model.