LRH: NELSON ET AL.

RRH: POPULATION DEMOGRAPHY OF WHITE STURGEON

Population Growth and Demography of White Sturgeon in the Lower Fraser River

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Abstract. —White sturgeon were formerly abundant in the lower Fraser River of British Columbia, but have been dramatically reduced by overfishing and habitat loss. Significant efforts have been put into collecting baseline abundance and demographic data over the past decade. However, much of the population biology is still unknown, thereby limiting the ability of managers to focus conservation efforts. For example, one of the pressing questions is the importance of slough habitats, which are used by young juveniles much more than older juveniles and adults. In the absence of direct estimates of birth and death rates, a valuable alternative is to infer these rates from data on population structure using demographic models. Here we fit an age-based model for white sturgeon to the available length-frequency data from slough and river habitats. Our analysis of the parameterized model indicates that the white sturgeon population in the lower Fraser River was declining through the 1980s and into the 1990s. We estimate a growth rate in the range of $\lambda=0.90$ to $\lambda=0.96$, which corresponds to a 4%–10% decrease in the population each year. This estimate agrees with an independent estimate of $\lambda=0.91$ derived using only catch-per-unit-effort data on juvenile white sturgeon from a slough habitat. Sensitivity analysis of the fitted population model reveals that juvenile survival has the largest influence on population growth. Thus, we infer that improving juvenile survival in the slough habitats is key to conserving this white sturgeon population. We feel that observational and experimental studies that focus on the survival of young juveniles will have the largest impact on our understanding of white sturgeon population biology

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Introduction

White sturgeon *Acipenser transmontanus* were once abundant in the lower Fraser River. In the 1800s commercial fisheries harvested hundreds of tons each year, but catches soon underwent a dramatic decline and have not recovered since. Researchers studying this population have argued that the collapse was caused by a combination of overfishing and habitat loss (Semakula and Larkin 1968; Echols and FRAP 1995)—an impact and fate shared by other sturgeon populations across North America (e.g., Collins et al. 2000). White sturgeon in the Fraser River have been under a catch-and-release mandate since 1994. It is currently listed as a species of special concern by the Canadian government, and the lower Fraser River population is classified by the provincial government of British Columbia as at risk.

A great deal of effort has been put into collecting baseline abundance and demographic data to try and understand the biology of this white sturgeon population (Lane and Rosenau 1997; RL&L 2000; Levings and Nelson 2003). Female white sturgeon in the lower Fraser River have an age to maturity of around 30 years (Semakula and Larkin 1968), which may make the population particularly vulnerable to overfishing (Powles et al. 2000). Adults appear to make extensive use of side-channel (slough) habitats for spawning, as indicated by radio-tracking and observations of fertilized eggs or hatched larvae (Perrin et al. 2003). Furthermore, available data show that young juveniles (~1-13 years old) are far more abundant in these sloughs than older juveniles (~14-30 years old), and adults (>30 years old) are only found in the river (Lane and Rosenau 1997). These studies suggest that white sturgeon in the Fraser River currently make use of two different habitats throughout their life.

While these data reveal some of the basic biology and habitat use for white sturgeon, they do little to help conserve the population. The data tell us nothing about vital rates of the population—such as the number of spawning adults, birth rates or death rates—all of which are required to understand population growth (Hilborn and Walters 1992; Caswell 2001; Rosenfeld 2003). This limits the ability of managers to focus conservation efforts. For example, are the slough habitats or river habitats more critical for population growth? Many researchers attempt to identify “critical habitat” based on where individuals spend their time (e.g., Gregr and Trites 2001). However, since such data provide no information about the population vital rates, it can lead to incorrect management strategies (e.g., Gunn and Sein 2000; Rosenfeld 2003). The best way to answer management questions is to have some knowledge of population vital rates. This allows an analysis of the current state of the population and provides definitive conservation strategies (e.g., Fujiwara and Caswell 2001).

Obtaining population birth and death rates is difficult in natural populations. In lieu of direct observations of these rates, a valuable alternative is to infer them by fitting a population model to the available abundance data (Nelson et al. 2004). Here we take such an approach and develop an age-based population model for white sturgeon that allows migration between two habitats. We fit the model to length-frequency distributions from slough and river environments, which we then analyze to assess the current state of the population and the most critical demographic stage. Throughout our model development, we highlight assumptions of the analysis and, where possible, explore the robustness of our conclusions.

Model Development

Data. —The data were obtained from two monitoring programs in the lower Fraser River that covered slough and river environments (McDonald et al. 1987, 1989; Lane and Rosenau 1997; RL&L 2000). We used data from the Nicomen slough (near Mission, British Columbia) to represent a typical slough habitat because it regularly contained an abundance of juvenile white sturgeon and was sampled intensively on five occasions (Lane and Rosenau 1997). Fish were caught in Nicomen slough in 1985, 1986, 1987, 1992, and 1993 using a consistent gill-net methodology. The river data were from two reaches of the Fraser River, pooled over four years and caught at a later time (1995-1998) than samples from the slough habitat (RL&L 2000). The first reach was between Mission and Hope (SG1), where the river had a braided channel with large side-channels that formed the slough habitats, including Nicomen slough. The second reach was between Hope and Hell's Gate (SG2) where the river was a single, fast-flowing channel with numerous rapids. River fish were caught primarily by angling, with only about 5% of the data coming from set-lines (RL&L 2000). The slough data included both catch-per-unit-effort (CPUE) and length-frequency distributions. However, the length frequency data alone were sufficient to estimate the population growth rate and the most critical demographic stages with our model, and we reserved the CPUE time-series from the slough as a means to independently test the model predictions.

The use of length-frequency data to parameterize our population model required that the data represent a stable length-frequency distribution (Caswell 2001). The length-frequency distributions in the Nicomen slough appeared similar among years (Figure 1). We assessed this statistically by looking for a change in the proportion of fish in each length category among years. Since each length-frequency distribution was considered a random sample from a multinomial distribution (with each length category representing a separate bin), stability was assessed by testing for a change in the multivariate proportions over time. We detected no statistically significant trend in the length-frequency distributions over time ($P>0.05$; VGAM library, Yee and Wild 1996; R statistical environment, Ihaka and Gentleman 1996). Thus, it was deemed reasonable to consider the slough data as estimates of a stable length-distribution for the population.

Since white sturgeon in the slough and river habitats are two components of the same population, the above conclusion that slough fish are at a stable length-distribution suggests the entire population is at a stable length-distribution. Therefore, we considered each of the five slough and two river samples as replicate observations of the population, and fit our population model to each combination (ten in total) to estimate the sensitivity of our conclusions to observation error.

Population boundaries. — The lower Fraser River starts below Hell's Gate, a velocity barrier that prevents upstream migration of white sturgeon, and ends at the Pacific Ocean. The analysis of mitochondrial DNA and microsatellite loci from white sturgeon in the lower Fraser River suggests that this is a single population (Smith et al. 2002). This conclusion is supported by mark-recapture studies that have found little movement of white sturgeon between lower and upper Fraser River (Toth et al. 2000; Yarmish et al. 2001). Thus, it is reasonable to consider this region of the river as a single population and ignore immigration and emigration in our model.

Estimating age from length. — In order to fit an age-based model to length-based data, we must define a growth function. We used a von Bertalanffy growth model:

$$\gamma(a) = L_\infty\left(1 - \exp(-ka)\right) \quad \textbf{(1)}$$

where γ(a) was predicted length at age *a*, and parameters L_∞ and *k* represented the asymptotic size and growth rate, respectively. Estimates of L_∞ (370 cm) and k (0.025 year^{-1}) were based on age data from the pectoral fin rays of 308 fish in the Fraser River (RL&L 2000). Paragamian and Beamesderfer (2003) argue that this method underestimates the true age of sturgeon by 30-60%. To examine the sensitivity of our conclusions to this methodological bias, we repeated the entire analysis with *k*=0.017 and an age of maturity of 45 years (we also tried *k*=0.0125 and an age-at-maturity of 60 years, but found the fit to data was poor).

Vulnerability to gear. —White sturgeon were caught in the slough using gill nets (Lane and Rosenau 1997) and in the river by angling and set-lines (RL&L 2000). Elliot and Beamesdefer (1990) compared the length-frequency distribution of these three catch methods using a population of white sturgeon in the Columbia River. They found that angling and set-lines tended to catch larger fish than gill-nets, suggesting that we need to consider different vulnerability functions for the slough and river data. The authors also observed that vulnerability increased in small white sturgeon to a point of saturation and then likely decreased again for large fish. However, the decline in the slough length-frequency distribution in our study occurred at a smaller size than observed in the study by Elliot and Beamsderfer (1990), suggesting that a vulnerability function that increased monotonically until saturation was appropriate for the slough habitat. Unfortunately, there was no way to disentangle the contribution of gear vulnerability and mortality to the decline in observed length-frequency distributions of larger fish in the river. We therefore take the common approach (e.g., Hilborn and Walters 1992) of assuming that vulnerability can be represented with a saturating function, and model the river habitat using a similar function as used in the slough. We consider the implications of this in our discussion.

We assumed that vulnerability could be described by a sigmoid function that increased with length (Hilborn and Walters 1992). We set the saturation value at one so that vulnerability represented the proportion of the true length-frequency distribution that could be caught. The vulnerability function was

$$v(l) = \frac{l^s}{L_h^s + l^s} \qquad \textbf{(2)}$$

where L_h was the length at which vulnerability was 0.5, s determined how quickly the transition occurred, and l was length. Since there was a separate vulnerability function for the slough and river habitats, there were four parameters in the model used to describe vulnerability (L_h and s for both habitats).

The model. —The model was an age-based density-independent matrix model that included migration between the slough and river habitats (Figure 2). Non-zero matrix elements represented fertility (the number of surviving young-of-the-year produced by each adult, F_B), annual survival in the slough (P_S), annual survival in the river (P_R), and annual migration between the slough and the river (P_M). Since all individuals have left the slough by age 25, and do not reach 100 years old in the river (Figure 3), we only modeled 25 years in the slough habitat and 100 years in the river habitat (Figure 4).

The model parameters were all likely affected by density-dependent processes, such as competition for food. However, there were no independent data available to parameterize density-dependence, nor were there sufficient temporal dynamics that could be used to infer density-dependence statistically. We therefore resorted to the following approach. We assumed that the population was well below historical levels, as a result of overfishing, such that current population rates were not strongly influenced by density-dependent factors over the time span that the data were collected. Since all parameters were constant per-capita rates, the resulting model was entirely density-independent, and only capable of exponential growth or decline. While such a model would be unrealistic for making long-term forecasts, it is a valuable approach for examining the current state and projected trajectory of a population (Caswell 2001).

The population vital rates (birth, death and migration) were assumed to be age-dependent. Unfortunately, little is known about age-specific patterns with the exception of age at maturity, which has been estimated to be from 26 to 34 years old in the Fraser River (Semakula and Larkin 1968) and was set at 30 years in the model. For example, it is well known that egg production increases with size (and thus age) of female white sturgeon (Semakula and Larkin 1968), but there were no data that could translate this into an estimate of the young-of-the-year that would recruit into the population. However, in contrast to the problem of density-dependent rates, the data can distinguish some age-dependence in the vital rates.

Most length-frequency distributions (e.g., Figure 1) are characterized by increasing frequency at young ages, reflecting the inability of fishing gear to catch small fish, followed by a decrease in the frequency of older fish, reflecting mortality (Hilborn and Walters 1992) and any decreases in catchability at large lengths. Since we assumed that gear performance was maximized (and constant) after the peak frequency, the decline with age reflected the combination of survival and population growth rate (Caswell 2001). Note that this is in contrast to traditional age- and length-based analyses (e.g., Hilborn and Walters 1992) that assume the population is at equilibrium (i.e. $\lambda=1$) such that the decline in frequency reflects only mortality (Hilborn and Walters 1992). Since our model makes no assumption about equilibrium, the mortality rates must be estimated at the same time as all other parameters by fitting the complete length-frequency distributions from both the slough and river habitats.

Estimates of age-frequency from the slough and river habitats were obtained from size data using a von Bertalanffy growth model with $k=0.025$ and $L_{\infty}=370$. The tail of each slough age-frequency distribution was a combination of mortality and migration from the slough to the river. Age-dependence in these two processes were too intertwined with length-specific vulnerability (discussed below) to be distinguished from the data. To allow for age-dependent loss from the slough distributions, we modeled slough migration as a linear function of age. The tail of each river age-frequency distribution was assumed to be the result of both survival and population growth. Since the asymptotic population growth rate is constant, any non-linearity on the log scale suggested that mortality rates were changing with age. To account for this potential age dependence, we represented river mortality as a linear function of age.

The resulting functions described the birth rate (F_B), annual survival in the slough (P_S), annual survival in the river (P_R), and annual migration between the slough and the river (P_M).

$$
\begin{aligned}
&F_B(a_r) = \begin{cases} 0 & \text{if } a_r < 30 \\ b & \text{if } a_r \geq 30 \end{cases} \\
&P_S(a_s) = \begin{cases} \exp(-\delta_s)\exp(-\mu_s(a_s)) & \text{if } a_s < 25 \\ 0 & \text{if } a_s \geq 25 \end{cases} \\
&P_M(a_s) = \begin{cases} \exp(-\delta_s)\left(1-\exp(-\mu_s(a_s))\right) & \text{if } a_s < 25 \\ \exp(-\delta_s) & \text{if } a_s = 25 \\ 0 & \text{if } a_s > 25 \end{cases} \\
&P_R(a_r) = \exp(-\delta_r(a_r))
\end{aligned}
$$

where a_s was age for fish in the slough, a_r was age for fish in the river, b was the number of young-of-the-year produced by each adult, $\mu_s(a_s)$ was the slough to river migration rate, δ_s was slough mortality rate, and $\delta_r(a_r)$ was the river mortality rate. All rates were instantaneous per capita rates. Slough migration and river mortality were modeled as linear functions of age:

$$
\begin{aligned}
\mu_s(a_s) &= \mu_o + \mu_a a_s \\
\delta_r(a_r) &= \delta_o + \delta_a a_r
\end{aligned}
$$

The resulting population model was described by the six parameters: b, δ_s, μ_o, μ_a, δ_o, and δ_a coupled to the four previous parameters that describe gear vulnerability.

Our goal was to understand current state of the population, its projected trajectory (increasing, decreasing or unchanging) and the demographic stage that had the most influence on population growth. We examined four models that varied in complexity (with and without age dependence in migration and mortality rates), but only present results for the variant with the lowest Akaike information criterion (AIC) value (Burnham and Anderson 2001).

Model fitting. —In order fit the age-based model to length-frequency data, the stable-age distribution ($\tilde{p}$) of **A** was predicted using the eigenvector of the dominant eigenvalue (see Caswell 2001 for a good reference to these methods). The predicted stable-length distribution was created by determining a corresponding length for each age, based on the growth function of Equation 1, and multiplying each age proportion by the vulnerability function of Equation 2 to get the gear corrected proportion ($\hat{p}_j$)

$$\hat{p}_j = \tilde{p}_j \left(\frac{l_j^s}{L_h^s + l_j^s} \right)$$

where j indexed age and l_j was the length of an age j fish (i.e., $l_j = L_\infty\left(1 - \exp\left(-kj\right)\right)$). These proportions were then summed into the length categories i of the observed data to produce the predicted length-distribution $\hat{p}_i$.

Model parameters were estimated by comparing the predicted and observed stable length-distributions. The probability distribution for the observed data was considered to be a multinomial sampling problem, with each length category a separate proportion. The most likely parameters were those that maximized the likelihood of the observed data, or equivalently, minimized the *deviance* equation (McCullagh and Nelder 1989). The deviance equation for our multinomial sampling problem was

$$D = 2\left(N_s \sum_{i=1}^{n_s} p_i \ln\left(\frac{p_i}{\hat{p}_i} \right) + N_r \sum_{i=1}^{n_r} p_i \ln\left(\frac{p_i}{\hat{p}_i} \right) \right) \qquad \mathbf{(3)}$$

where p_i was the observed proportion in length class i, $\hat{p}_i$ was the predicted proportion, N_s was the number of fish caught in the slough sample, N_r was the number of fish caught in the river sample, and n_x was the number of length categories in either the slough (s) or river (r) samples. The first summation covered all length classes in the slough, and the second all length classes in the river. The most likely parameters were found by numerically searching for the minimum of Equation 3. Minimization was completed using OPTIM in the R statistical environment (Ihaka and Gentleman 1996) through a constrained quasi-Newton routine.

The parameterized model allowed us to estimate the current population growth and the demographic stage that had the most influence on population growth. As mentioned above, the asymptotic growth of the population model (λ) was determined by computing the dominant eigenvalue. If λ was greater than one, the population was increasing; if λ was equal to one, population abundance was constant through time; and if λ was less than one, the population was decreasing. Population growth represented the balance between birth rates and death rates, but did not give any indication as to which stage or age was most valuable. This was determined by looking at the *elasticities* of λ (Caswell 2001). Elasticities are the proportional changes in λ that occurred from a proportional change in the vital rates, and were computed from the eigenvectors of the dominant eigenvalue (Caswell 2001). The age or stage that caused the largest elasticity in λ had the greatest influence on the current population growth, which we referred to as the most *critical demographic stage*. We used these two quantities, λ and the critical demographic stage, to understand the status of the population and to suggest focused conservation strategies.

The final issue to be considered was non-uniqueness. As is common when attempting to estimate birth and death rates from state abundances, there were many combinations that fitted the length-distribution data equally well. This non-uniqueness in parameters can be a formidable barrier to inverse methods (Nelson et al. 2004). However, since we were not interested in the rates themselves, but rather the population growth rate λ and most critical demographic stage, we contended with non-uniqueness by determining these values for *every* combination of birth and death rates supported by the data. Fortunately, in our situation the birth and death rates were only partially non-unique because very low and high birth rates were not supported by the data. Thus, for each of the ten data set combinations, we set the birth rate and fit all remaining parameters. We systematically varied the birth rate from 0.01 onwards until the basin of non-uniqueness (from Equation 3) was well defined. Our conclusions are based on the most conservative estimate of λ and demographic structure over this range of parameter values.

Results

Log-scale age-frequency distributions appeared to be distinctly non-linear in both slough and river habitats (Figure 3). Assuming that the slough mortality rate was constant, the increasing slope at older ages (Figure 3a) would reflect the additional losses due to migration. Non-linearity in riverine age-frequency distributions was apparent for fish older than age 25-35, which suggested that it was not related to a difference between slough and river mortality rates, but rather to an increased mortality rate of the adults in the river.

The model captured the length-frequency distributions well in both slough and river habitats (Figure 5). AIC values from the four model variants (Table 1) suggested that the model with age-dependent mortality in the river habitat was best supported by the data (Burnham and Anderson 2001). We also fitted simpler versions of the model, such as assuming that mortality rates or vulnerability functions were the same in both slough and river habitats. However, these simpler models produced qualitatively poor fits to the data, suggesting the current model was a minimally complex model for the available data. Furthermore, while we only presented results for the model with age-dependent mortality in the river habitat (i.e., the best-fit model), we repeated the full analysis on all model variants and found our conclusions robust .

The parameterized model suggested that the lower Fraser River white sturgeon population was in decline from the mid 1980s to the mid 1990s. This observation was based on the estimated values of λ obtained for all combinations of slough and river samples (Figure 6). Each value of λ was the maximum value consistent with the data, over the range of non-unique estimates. We used the maximum λ to represent population growth as it was the most conservative with respect to erroneously predicting a population decline. As an example, Figure 6a shows the λ and deviance values (Equation 3) estimated from the 1987 slough data and the SG2 river data. The deviance values clearly show the region of non-uniqueness between birth and death rates. While this region was finite, it included a range of λ values that could not be distinguished by the data. Figure 6b summarizes the λ values from all ten model fits. The five slough estimates were assumed to be replicate observations of the stable length-distribution, so we used those data to compute confidence intervals (Figure 6c). The average λ for SG1 was 0.90, and the average λ for SG2 was 0.96. Since the confidence intervals did not include λ=1, the data suggested that the white sturgeon population declined by a conservative estimate of 4%-10% per year in the lower Fraser River.

The catch-per-unit-effort (CPUE) data from five sampling years in the Nicomen Slough (Lane and Rosenau 1997) provided an independent estimate of population growth (Figure 7). The slough was sampled over four months in each year, with use in each month declining through the season. Based on a linear regression with a common population slope for all months, there was a significant decline in CPUE over the nine years of sampling. In close agreement with the conclusions from our modeling analysis, the estimated annual rate of decline in CPUE was 0.91.

The demographic stage with the greatest influence on population growth was estimated by calculating the elasticity of λ to survival, fertility, and migration. Elasticities were computed for all ages, and represent the contribution of each vital rate to changes in the overall population growth rate (Figure 8). We have grouped elasticities into juvenile survival, adult survival, and fertility. Juvenile survival has the largest relative impact on population growth, accounting for 82% of the elasticity in λ compared to 15% for adult survival and 3% for fertility.

Elasticities reveal which vital rates have the greatest relative potential to change population growth. However, these are only valid for the current population state and can change quickly as growth rate changes (Caswell 2001) (e.g., if the population rebounds from conservation efforts). This may limit the ability of elasticities to reliably predict the best conservation strategy (e.g. Mills et al. 1999). To check the robustness of our conclusion that juvenile survival has the largest relative impact on current population growth, we systematically increased juvenile survival, adult survival and birth rate (each individually) from a reference set of vital rates. Juvenile survival always contributed between 80%-90% to the change in population growth, independent of the magnitude of λ or which vital rate was increased.

To investigate the importance of slough habitats, we further divided juvenile survival into slough and river components. Our estimates of the current population state indicated that juvenile survival in the river contributed about 75% to population growth, whereas juvenile survival in the sloughs only contributed about 5%; this suggested that survival in the river was much more important. However, in contrast to total juvenile survival, slough and river elasticities changed rapidly with increasing population growth and depended on which vital rate was changed. Not surprisingly, we found that if river survival was increased, rivers became more important; but, if slough survival was increased, sloughs became more important.

The importance of juvenile survival in slough versus river habitats can be more properly addressed by considering the change in each that would be required to achieve a target population growth rate (e.g., Fujiwara and Caswell 2001). We arbitrarily chose a target λ of 1.05 (i.e., we are aiming for a population that increases 5% each year). Figure 9 shows an example of how λ responded to changing juvenile survival in the river and slough habitats. Each line was generated by holding all other parameters constant and varying only one of the two mortality rates. The gradient of each line represented the change in lambda with the vital rate, which is the non-standardized form of elasticity (i.e., sensitivity). Two things are evident. Firstly, decreasing juvenile mortality in the river can *never* achieve a positive population growth rate, simply because the probability of survival is already near one. Secondly, an increase in slough survival of about 50% would be sufficient to stop the population from declining (λ=1) and a ~60% increase would increase population growth to 5% per year (λ=1.05).

Discussion

Analysis of the density-independent age-structured population model suggests that the white sturgeon population in the lower Fraser River was declining by 4% to 10% per year through the 1980s and into the 1990s. These conclusions are not sensitive to model details such as age-dependency in slough migration and river mortality, or variation among years in the observed data. Furthermore, reanalysis of the data with a 30% slower individual growth rate (k=0.017 and age at maturity of 45 years) had little impact on the results, causing the estimated λ to only increase by 0.03 (an estimated population decline of 4%- 7% per year). This suggests a degree of robustness to the model parameterization and analysis. In agreement with our model analysis, the independent CPUE data from the slough habitats show a decline of ~9% per year. The close agreement between the analysis of the length-frequency and the independent CPUE data lends credence to the modeling process and its use in understanding population demography.

The best fit to the observed length-frequency data was obtained from a model with an increasing mortality rate for older white sturgeon within the river. Support for this is evident in the raw data as the log-decrease in age-frequency in the river habitats was distinctly non-linear. Such patterns are contrary to life-history theory that predicts slow-growing and late-maturing individuals to have a low adult mortality rate until senescence (Heppell et al. 2000). However, since the transition occurs very near the age of maturity, the increased mortality could be reflective of spawning activities. All modeling approaches have inherent assumptions that could affect the results. For example, we have taken the standard approach and assumed that gear vulnerability does not decrease for large fish (e.g., Hilborn and Walters 1992). But, if in reality it does (e.g., Rudstam et al. 1984; Elliot and Beamesderfer 1992), then the decreasing tail of the river age-frequency distribution will reflect both age-specific mortality and decreasing vulnerability. Unfortunately, there is no way to tease apart these possibilities with the available data. In our model, ignoring decreased gear vulnerability would cause an inflated estimate of river mortality and an underestimate of the population growth. However, the impact on the estimated population growth is minimal because adult survival contributes much less than juvenile survival, and the data still support a decreasing population. Furthermore, since our model conclusions are supported by independent observations of CPUE in the slough habitat, we believe that the results are robust.

The elasticity of λ reveals which vital rates have the greatest potential to change population growth. From our analysis of lower Fraser River white sturgeon, juvenile survival contributes to more than 80% of the potential change in λ, far outweighing adult survival and fertility. The disproportionate importance of juvenile survival is a common result for organisms with long ages to maturity (Heppell et al. 2000). Our analysis suggests that conservation efforts should focus on ways to reduce mortality in juvenile stages.

One of the pressing conservation issues for white sturgeon is the importance of slough habitats—particularly because these habitats are under significant amounts of development pressure (e.g., Schreier et al. 1991). By comparing the role of juvenile survival in the slough versus river habitats, it is clear that juvenile survival in the slough habitat is key to conservation of the population because decreasing the mortality rate of juveniles in the river could not prevent the population from continued decline. As a result, we argue that juvenile survival in the slough habitat should be considered the most critical demographic stage for white sturgeon in the lower Fraser River.

In conclusion, two lines of evidence indicate that white sturgeon in the lower Fraser River were declining by 4%-10% per year over the period 1985-1993. More recent length-frequency data would be invaluable to track current population growth. However, since white sturgeon have a long age-to-maturity, and there is difficulty in observing small fish, it may take some time for conservation efforts to be reflected in the length-frequency data. Our analysis fits a density-independent model to observed length-frequency data. The close agreement between the results of the length-frequency analysis and the independent estimates of CPUE in the slough, suggests that the parameterized model captures a reasonable snapshot of the population vital rates and demographics. With this support, our analysis provides the following guidance to conservation efforts. The most likely way to increase population growth is to increase juvenile survival. If younger juvenile white sturgeon (0-13 years old) continue to make use of slough environments, as suggested by available data, then these habitats will be essential to the conservation and recovery of white sturgeon in the lower Fraser River. Conservation efforts would further benefit from observational and experimental work that aim to understand the causes of mortality in different juvenile age groups. In particular, studies that quantify the mortality rate of young juveniles in slough and river habitats will not only provide data to evaluate our analysis, but will contribute significantly to understanding the ecology of this valuable resource.

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Footnotes

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Table 1. —AIC delta values between the four model variants. The example shown are for a fertility of 10. Model C has the lowest AIC value.

Model Variant	Age dependent migration	Age dependent river mortality	Number of Parameters	ΔAIC[*]
A	N	N	7	-
B	Y	N	8	0
C	N	Y	8	-15.1
D	Y	Y	9	-12.9

*The difference in AIC value between the least complex model and the models with more parameters.

Figure Legends

Figure 1. —Observed length-frequency distributions for white sturgeon collected in the Nicomen Slough and the lower Fraser River. The SG1 data are from the length of river between Hope and Mission, and the SG2 data are from the river between Hell’s Gate and Hope. Data are from Lane and Rosenau (1997) and RL&L (2000).

Figure 2. —Age-based density-independent matrix model that includes migration between slough and river habitats. Elements of the projection matrix (***A***) represent the transition from one age to the next and migration between the slough and river. As a result, most of the transitions are zero except for the four functions that describe fertility (the number of surviving young-of-the-year produced by each adult, F_B), annual survival in the slough (P_S), annual survival in the river (P_R), and annual migration between the slough and the river (P_M). The grey arrows show age structure within either the slough or river environments.

Figure 3. —Log_e age-frequency distributions from the age with the peak frequency onwards for a) Nicomen slough and b) the Fraser River.

Figure 4. —Graphical description of the population model. Boxes represent the slough and river habitats and arrows represent the vital rates. The vertical lines in each box represent white sturgeon age within the habitat, with grey representing the adults. All rates are per capita and the (*age*) designation means that the parameter can change with age. Since spawning occurs in the sloughs, all young-of-the-year white sturgeon are introduced into the slough habitat. As fish age, they suffer a constant mortality rate and probability of migrating to the river habitat. Once in the river habitat, they suffer an age-dependent mortality rate. Reproduction occurs once the individuals have reached a fixed age at maturity.

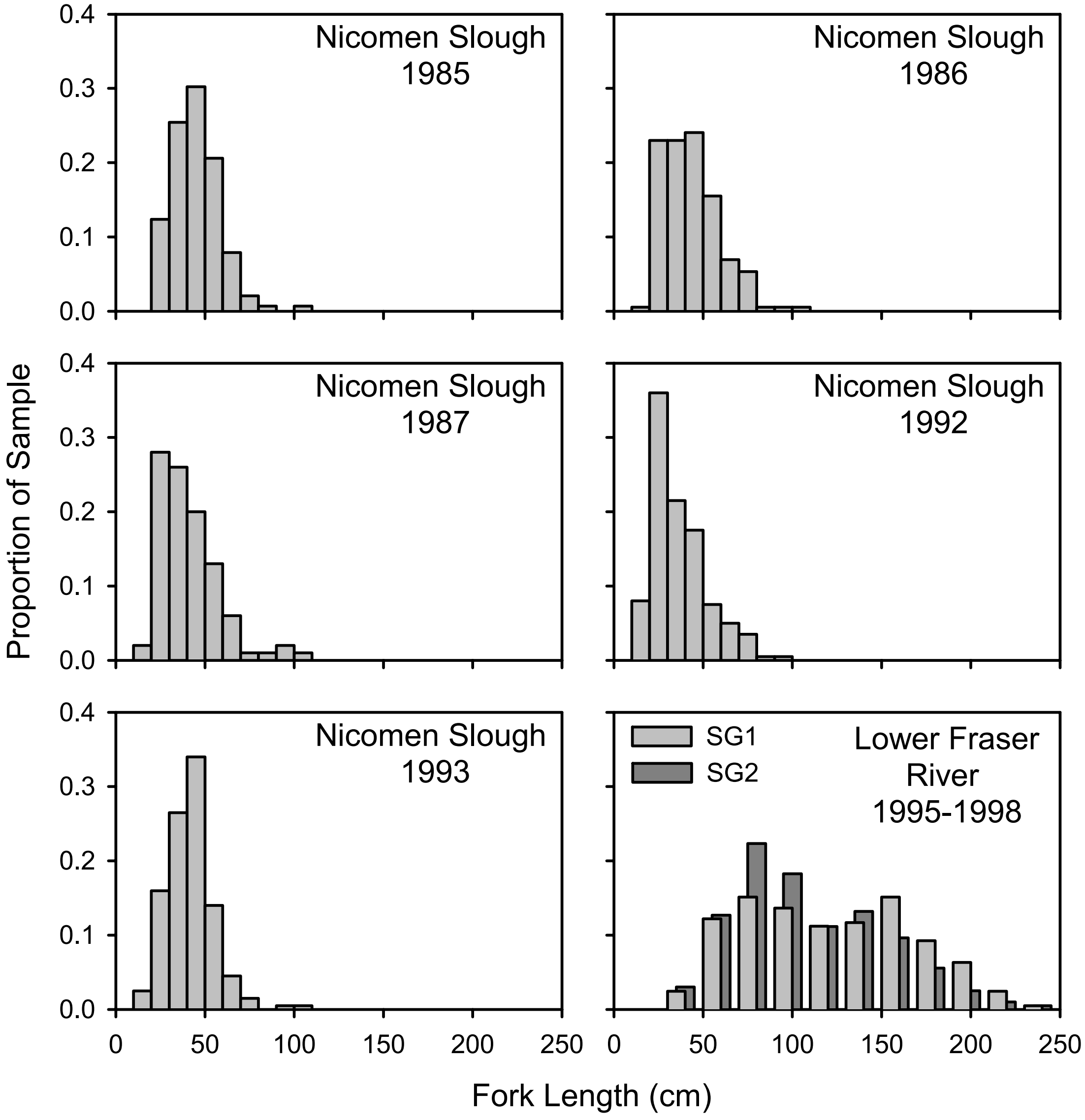
Figure 5. —Example model fits to the data with a fixed birth rate of 10. Black circles represent the slough data, light grey circles represent the SG1 river data, and dark grey circles represent the SG2 river data. Grey lines are fits to each combination of slough data and SG1, and black lines are fits to each combination of slough data and SG2.

Figure 6. —Estimated population growth rates. a) Example deviance values and estimated population growth (lambda, λ) as a function of birth rate from fits to 1987 slough data and SG2 river data. The region of non-uniqueness between birth and death rates is highlighted with a grey background. b) The range and maximum λ for each combination of slough year and river data set. The ranges are from the estimated λ values over the non-unique region. c) Average of the maximum population growth rates for each of the two river data sets. The error bars are 95% confidence intervals from each the five slough years. Example parameter estimates are b=51, δ_s=0.83, δ_r=0.054+0.0051*a_r, μ_s=0.0154, S_s=7.8, L_{hs}=48.51, S_r=8.9, L_{hr}=65.26.

Figure 7. —Catch per unit effort (CPUE) in the Nicomen Slough. Data are from Lane and Rosenau (1997).

Figure 8. —Estimated population elasticities. a) Example elasticities in λ for juvenile and adult survival (black line), and for the birth rate (grey line) from fits to 1987 slough data and SG2 river data. b) Average and range of the elasticity for each slough year and river data set. Circles represent juvenile survival, diamonds adults survival, and triangles the birth rate. c) Average elasticities in λ for juvenile survival, adult survival, and birth for each of the two river data sets. Error bars are 95% confidence intervals from each of the five slough years.

Figure 9. —Change in population growth (λ) with change in juvenile survival. The grey line is survival in the slough and the black line is survival in the river. The circles are the estimated vital rates from fits to 1987 slough data and SG2.



Nicomen Slough 1985
Nicomen Slough 1986
Nicomen Slough 1987
Nicomen Slough 1992
Nicomen Slough 1993
Lower Fraser River 1995-1998
SG1
SG2
Proportion of Sample
0.0
0.1
0.2
0.3
0.4
0
50
100
150
200
250
Fork Length (cm)

Figure 1

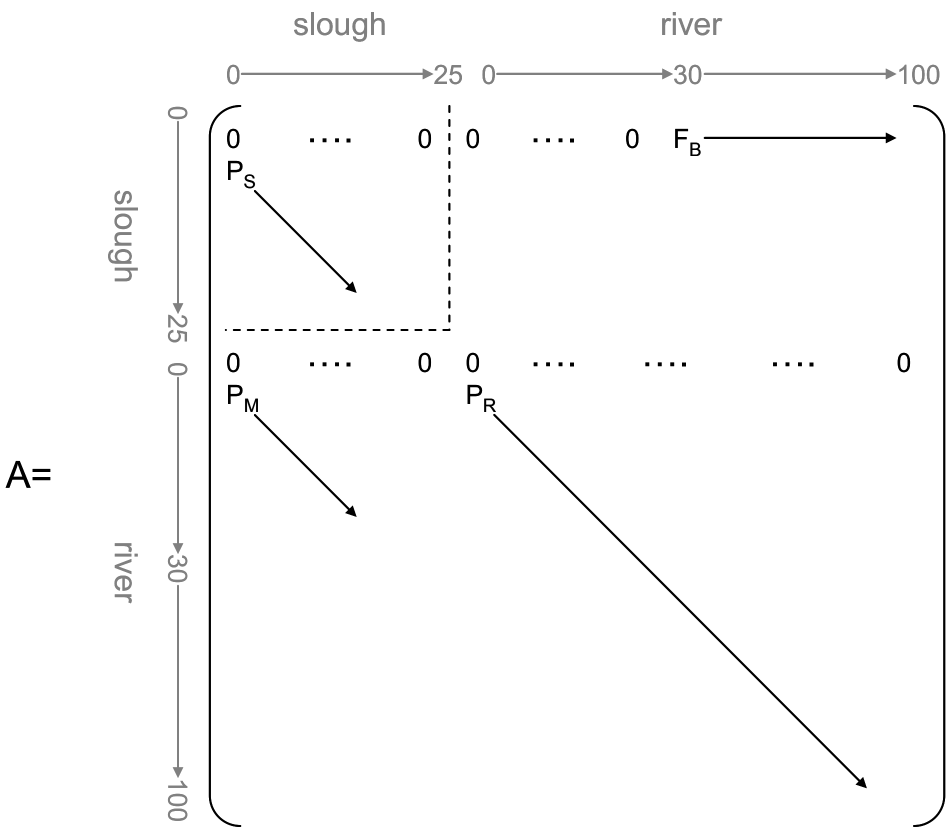
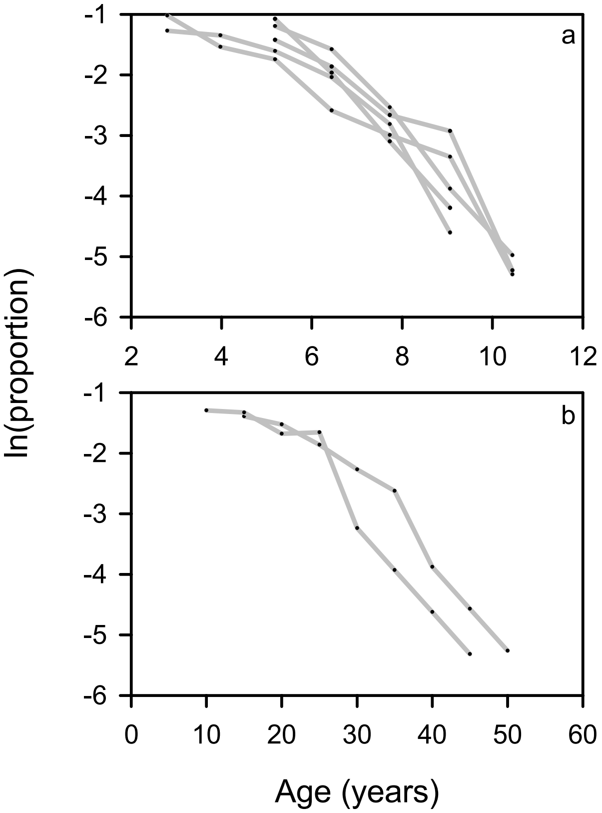


Figure 2



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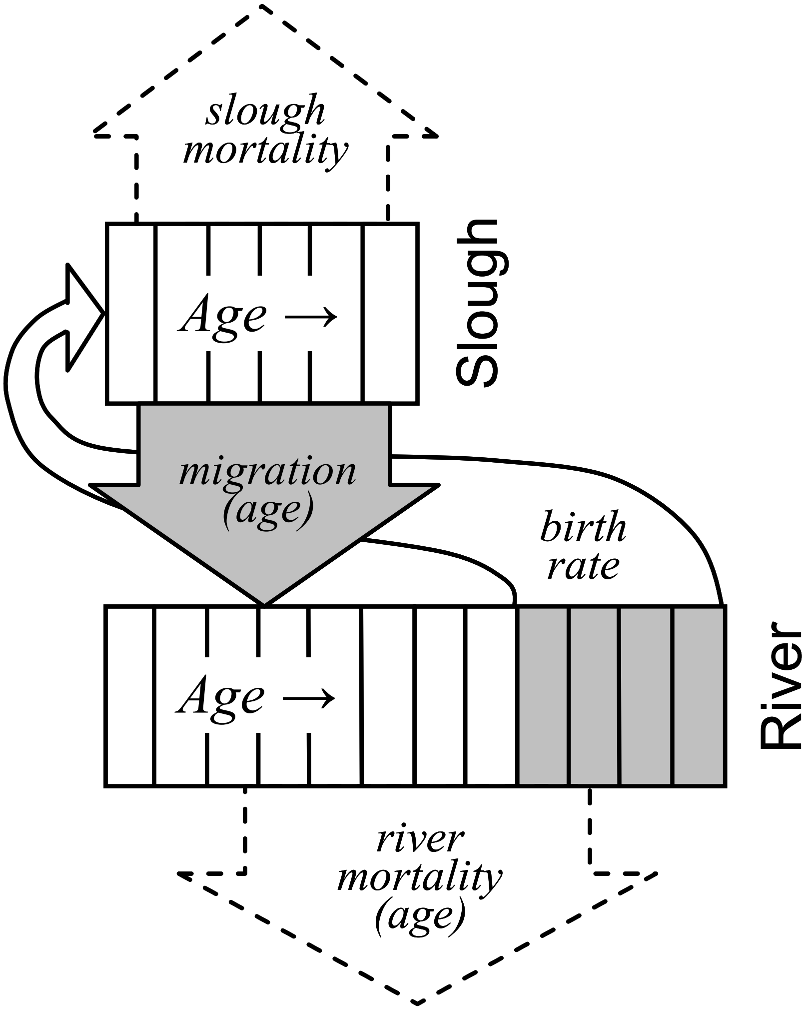

slough mortality
Slough
Age →
migration (age)
birth rate
River
Age →
river mortality (age)

Figure 4

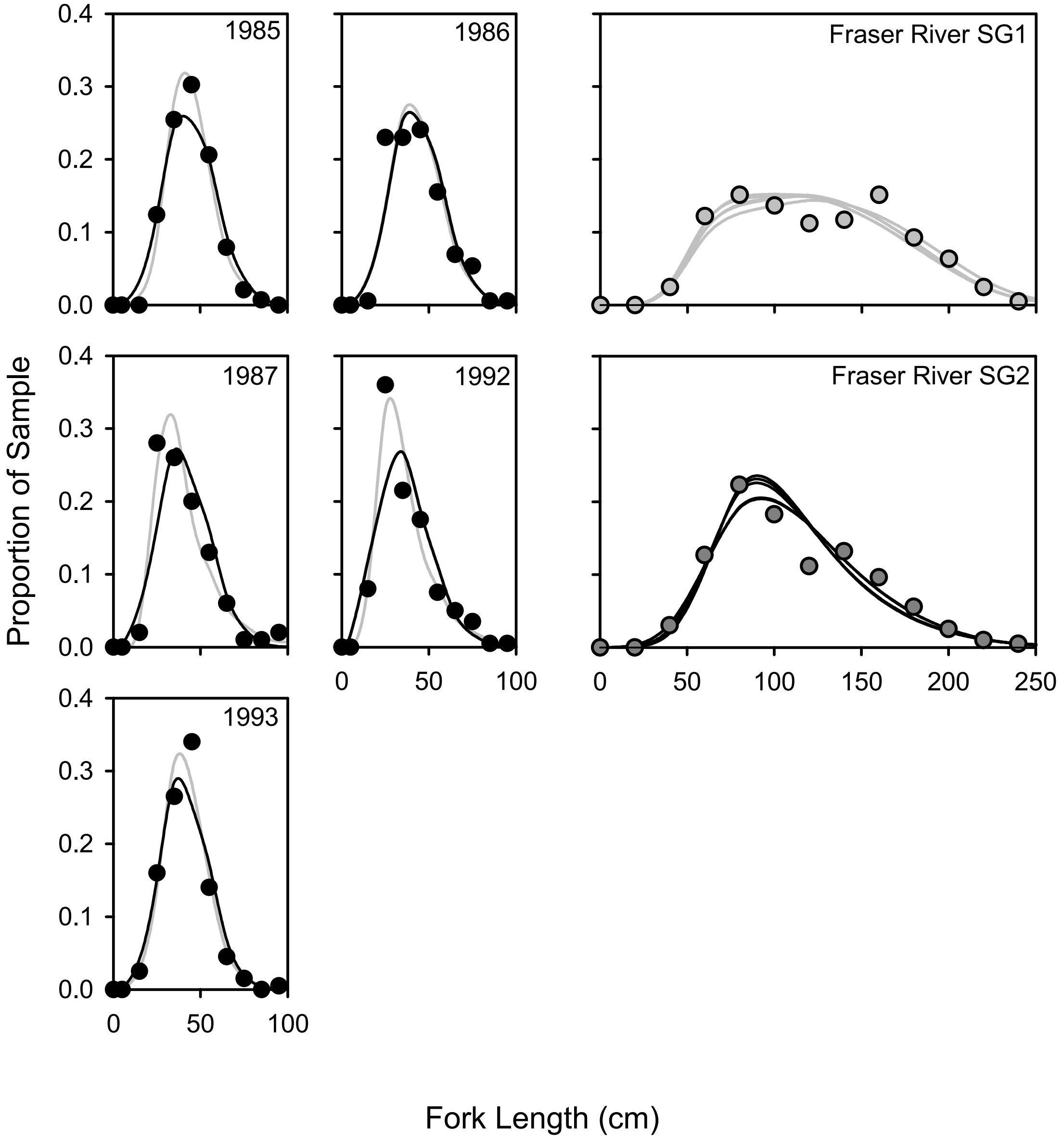
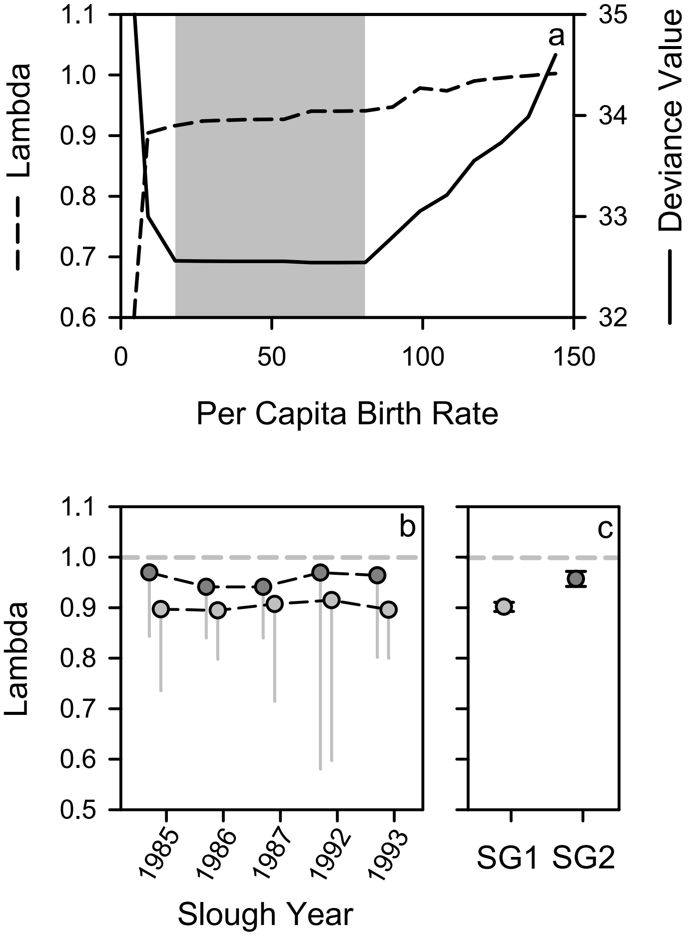

1985
1986
Fraser River SG1
1987
1992
Fraser River SG2
1993
Proportion of Sample
0.0
0.1
0.2
0.3
0.4
0
50
100
150
200
250
Fork Length (cm)

Figure 5



a
Lambda
Deviance Value
1.1
1.0
0.9
0.8
0.7
0.6
35
34
33
32
0
50
100
150
Per Capita Birth Rate
b
c
Lambda
1.1
1.0
0.9
0.8
0.7
0.6
0.5
1985
1986
1987
1992
1993
Slough Year
SG1
SG2

Figure 6

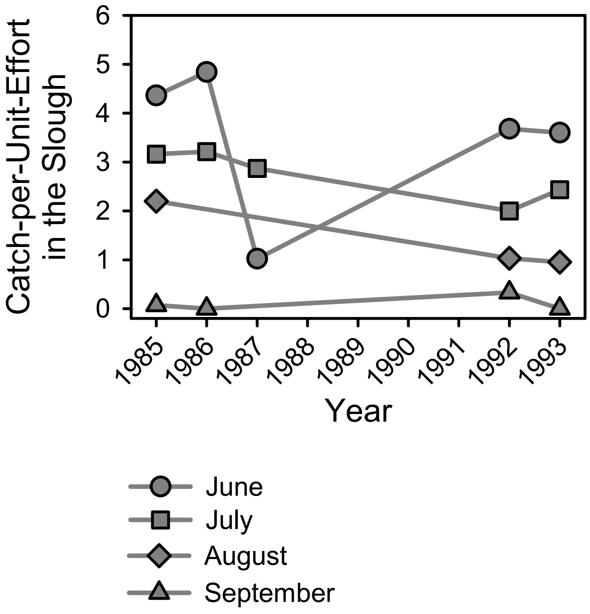

Catch-per-Unit-Effort in the Slough
6
5
4
3
2
1
0
1985
1986
1987
1988
1989
1990
1991
1992
1993
Year
June
July
August
September

Figure 7

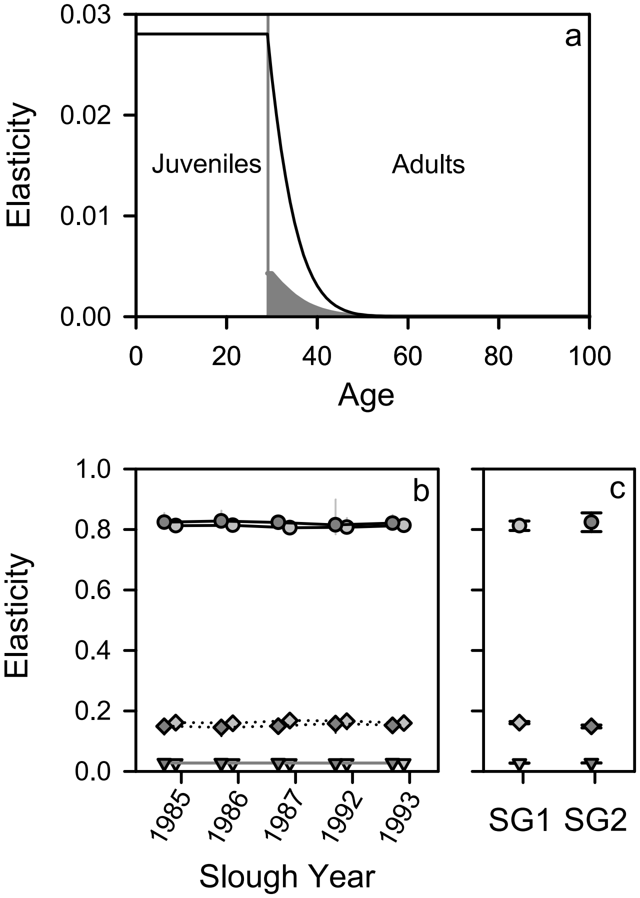

0.03
0.02
0.01
0.00
Elasticity
a
Juveniles
Adults
0
20
40
60
80
100
Age
1.0
0.8
0.6
0.4
0.2
0.0
Elasticity
b
1985
1986
1987
1992
1993
Slough Year
c
SG1 SG2

Figure 8

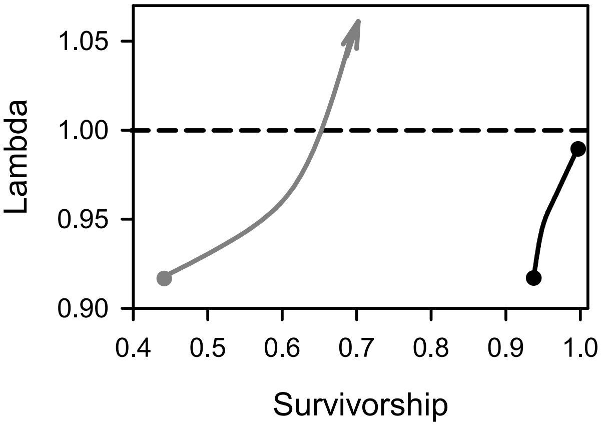


Figure 9