

Fisheries and Oceans Canada Pêches et Océans Canada

Ecosystems and Oceans Science Sciences des écosystèmes et des océans

Canadian Science Advisory Secretariat (CSAS)

Research Document 2016/032

Maritimes Region

Recovery Potential Assessment for Outer Bay of Fundy Atlantic Salmon (Salmo salar): Population Dynamics and Viability

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Foreword

This series documents the scientific basis for the evaluation of aquatic resources and ecosystems in Canada. As such, it addresses the issues of the day in the time frames required and the documents it contains are not intended as definitive statements on the subjects addressed but rather as progress reports on ongoing investigations.

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Published by:

Fisheries and Oceans Canada Canadian Science Advisory Secretariat 200 Kent Street Ottawa ON K1A 0E6

http://www.dfo-mpo.gc.ca/csas-sccs/ csas-sccs@dfo-mpo.gc.ca



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Correct citation for this publication:

Gibson, A.J.F., Jones, R.A. and MacAskill, G.J. 2016. Recovery Potential Assessment for Outer Bay of Fundy Atlantic Salmon (*Salmo Salar*): Population Dynamics and Viability. DFO Can. Sci. Advis. Sec. Res. Doc. 2016/032. v + 87 p.

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ABSTRACT

The purpose of this research document is to provide information about the population dynamics and viability of Outer Bay of Fundy Atlantic Salmon in support of recovery planning for this designatable unit. It covers the topics in the Terms of Reference for the Recovery Potential Assessment for Outer Bay of Fundy Atlantic Salmon relating to estimation of age- and stagespecific life history parameters (mortality rates and stage transition probabilities), the past and present population dynamics and viability of these populations, and scenario analyses to help identify and prioritize among recovery actions.

Analyses are presented for the Nashwaak River and the Tobique River salmon populations. For the Nashwaak River population, life history parameter estimates were obtained by fitting a life history model to population-specific data including: annual estimates of juvenile densities; egg depositions; the number and age composition of emigrating smolts; and the numbers of returning adults. The results indicate that at-sea survival for salmon maturing after two winters at sea has decreased by a factor of about two to three, whereas recent increases in the return rates for salmon maturing after one winter at sea are nearer the historical values. Maximum lifetime reproductive rates decreased from an average of 2.49 in the 1970's to 1.13 in the 2000's for the Nashwaak River population, and was estimated to be 0.18 for the Tobique River population using data from 1989 to 2005. Based on these values, in the absence of human intervention or a change in these rates, the Tobique River population is expected to extirpate, whereas, although the Nashwaak River population has a equilibrium population size greater than zero, it has very little capacity to rebuild and is at risk of extirpation from random variability and stochastic events.

Population viability analyses indicate that relatively small increases in either freshwater productivity or at-sea survival are expected to markedly decrease extinction probabilities for the Nashwaak River population, although larger changes in at-sea survival will be required to restore the population to levels above their conservation requirements. Larger changes in survival are expected to be necessary to prevent the extirpation of the Tobique River population due to the reduced rate of survival for emigrating smolts.

Évaluation du potentiel de rétablissement (EPR) du saumon de l'Atlantique (Salmo salar) de l'extérieur de la baie de Fundy : Analyses de la viabilité de la population

RÉSUMÉ

Le présent document de recherche a pour objet de fournir des renseignements à propos de la dynamique et de la viabilité des populations du saumon de l'Atlantique de l'extérieur de la baie de Fundy à l'appui de la planification du rétablissement de cette unité désignable. Il traite des points du cadre de référence pour l'évaluation du potentiel de rétablissement du saumon de l'Atlantique de l'extérieur de la baie de Fundy relatifs à l'estimation des paramètres du cycle biologique propres à l'âge et au stade (les taux de mortalité et les probabilités de transition de stades), à la dynamique des populations passées et présentes et à la viabilité de celles-ci, et aux analyses de scénarios afin d'aider à définir des mesures de rétablissement et à établir des priorités entre elles.

Les analyses sont présentées pour les populations de saumons des rivières Nashwaak et Tobique. Les estimations des paramètres du cycle biologique de la population de la rivière Nashwaak ont été obtenues en intégrant un modèle de cycle biologique aux données d'une population précise, notamment les estimations annuelles des densités de juvéniles, les pontes, le nombre et la composition selon l'âge des saumoneaux qui émigrent et le nombre d'adultes qui reviennent. Les résultats montrent que le taux de survie en mer des saumons qui atteignent la maturité après avoir passé deux hivers en mer a diminué d'un facteur d'environ deux à trois. tandis que les récentes augmentations dans les taux de montaison de saumons qui atteignent la maturité après avoir passé un hiver en mer sont plus proches des valeurs historiques. Les taux de reproduction maximaux ont diminué, passant d'une moyenne de 2,49 dans les années 1970 à 1,13 dans les années 2000 pour la population de la rivière Nashwaak, et ils ont été estimés à 0,18 pour la population de la rivière Tobique à l'aide des données de 1989 à 2005. En fonction de ces valeurs, en l'absence d'une intervention humaine ou d'un changement dans ces taux, on s'attend à ce que la population de la rivière Tobique disparaisse. De son côté, bien que sa taille à l'équilibre soit supérieure à zéro, la population de la rivière Nashwaak a une faible capacité de rétablissement et elle est à risque de disparition en raison de la variabilité aléatoire et d'événements stochastiques.

Selon des analyses de viabilité démographiques, des augmentations relativement faibles de la productivité en eau douce ou de la survie en mer devraient permettre de grandement réduire les probabilités de disparition de la population de la rivière Nashwaak, même si des changements plus importants sur le plan de survie en mer seront nécessaires pour rétablir la population à des niveaux supérieurs à ceux qui sont requis pour sa conservation. En revanche, des changements plus importants concernant la survie devraient être nécessaires pour empêcher la disparition de la population de la rivière Tobique en raison du faible taux de survie des saumoneaux qui émigrent.

1.0 INTRODUCTION

The Outer Bay of Fundy Designatable Unit of Atlantic Salmon (*Salmo salar*) occupies rivers in New Brunswick between the Canada-USA border and the city of Saint John, including the Saint John River (Figure 1). This designatable unit was designated as "endangered" by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC 2011). To aid in consultative processes following the designation, and to serve as a basis for recovery planning, information about Outer Bay of Fundy Atlantic Salmon populations has been compiled in support of the Recovery Potential Assessment (RPA) for this designatable unit, addressing the 27 Terms of Reference (TORs) developed to guide the process.

This research document contains information about the population dynamics of Outer Bay of Fundy Atlantic Salmon, including:

- 1. life history parameters such as stage-specific mortality rates and stage transition probabilities;
- 2. the past and present population dynamics;
- 3. population viability; and
- 4. scenario analyses to identify and prioritize among recovery actions.

This information is based on new analyses of data from the Nashwaak River salmon population and a summary of previously published information about the dynamics of the Tobique River salmon population.

Specifically, this document addresses the following TORs:

- 1. Estimate, to the extent that information allows, the current or recent life-history parameters (total mortality, natural mortality, fecundity, maturity, recruitment, etc.) or reasonable surrogates; and associated uncertainties for all parameters.
- Project expected population trajectories over three generations (or other biologically reasonable time), and trajectories over time to the recovery target (if possible to achieve), given current parameters for population dynamics and associated uncertainties using Fisheries and Oceans Canada (DFO) guidelines on long-term projections (Shelton et al. 2007).
- 3. Assess the probability that the recovery targets can be achieved under current rates of parameters for population dynamics, and how that probability would vary with different mortality (especially lower) and productivity (especially higher) parameters.
- 4. Project expected population trajectory (and uncertainties) over three generations (or other biologically reasonable time), and to the time of reaching recovery targets when recovery is feasible; given mortality rates and productivities associated with specific scenarios identified for exploration (as above). Include scenarios which provide as high a probability of survivorship and recovery as possible for biologically realistic parameter values.
- 5. Recommend parameter values for population productivity and starting mortality rates, and where necessary, specialized features of population models that would be required to allow exploration of additional scenarios as part of the assessment of economic, social, and cultural impacts of listing the species.
- 6. Evaluate maximum human-induced mortality which the species can sustain and not jeopardize survival or recovery of the species.

2.0 INFORMATION ABOUT LIFE HISTORY

COSEWIC (2011) identified 17 rivers considered to contain, or historically to have contained Outer Bay of Fundy Atlantic Salmon, although it is likely salmon may have used the smaller coastal or un-assessed rivers in southwest New Brunswick as well (Marshall et al. 2014). Although there is some variability in life history characteristics, the life cycle of Atlantic Salmon is relatively similar among populations throughout the region. In this section of the research document, the life cycle is described, estimates of life history parameters considered representative of populations in the region are provided, and these estimates are used to characterize the dynamics of the populations both in the past and at present. Specifically, information is provided about the life cycle of Atlantic Salmon, which served as the basis for the population models (Section 2.1) and the life history parameter values for the Nashwaak River and Tobique River populations derived using a statistical, life history-based population model (Section 2.2).

2.1 LIFE CYCLE OF OUTER BAY OF FUNDY ATLANTIC SALMON

Outer Bay of Fundy Atlantic Salmon are anadromous fish, meaning that while they are obligated to reproduce in fresh water, most spend part of their lives in the ocean to feed and grow. They are iterparous, meaning that they can spawn several times before they die. After spawning for the first time, some individuals may spawn again in consecutive years, while others may spawn in alternate years and others may switch between alternate and consecutive repeat spawning. Spawning typically occurs in late October and early November. After spawning, adults (known as "kelts") may return to the sea or may remain in fresh water until the following spring. Eggs are deposited in nests (referred to as "redds") excavated in the gravel substrate. Hatching begins in April and the yolk-sac larvae (known as "alevins"), remain in the gravel until May or June. After emergence from the gravel, the young (now called "fry") begin feeding. As they grow, their behaviour changes and they tend to be found in different places in the river. By autumn, they are referred to as "parr". Wild-origin parr in Outer Bay of Fundy rivers typically remain in fresh water for 2 to 4 years, although as described in Section 2.3, most leave the rivers at age-2 or age-3. Prior to leaving the river, parr undergo physical changes that allow them to survive in the ocean. These juvenile salmon are now referred to as "smolt" and will migrate to the sea during late April, May and early June. Timing of the smolt run varies somewhat with environmental conditions. Some male parr become sexually mature at a small size while still in the river (these are called "precocious parr" and are not included in the population model).

Within Outer Bay of Fundy populations, salmon mature after either one or two winters at sea (called "one sea-winter salmon" or 1SW, "two sea-winter salmon" or 2SW, respectively), although historically a small proportion also matured after three winters at sea (called "three sea-winter salmon" or 3SW). The proportion of salmon maturing after a given number of winters at sea can be highly variable among salmon populations, although populations in the Outer Bay of Fundy typically have a higher incidence of maturity as 2SW salmon than do salmon of the Inner Bay of Fundy designatable unit, which have a higher incidence of maturity as 1SW salmon. Three sea-winter salmon are now very rare or absent from most populations in the Outer Bay of Fundy. Adult run timing is variable. The terms "small salmon" and "large salmon" are used at times. Small salmon are <63 cm fork length and are virtually all 1SW salmon. Large salmon are >63 cm fork length, and include 2SW salmon, 3SW salmon as well as repeat spawning salmon ("multi-sea-winter" or MSW). A very small component of 1SW salmon may be greater than 63 cm fork length, but these are rare in the Outer Bay of Fundy. Similarly, a small component of the 1SW repeat spawning salmon may be less than 63 cm fork length, but these are also rare.

2.2 ESTIMATION OF LIFE HISTORY PARAMETERS

Life history parameter estimates were derived using a statistical, life history-based population dynamics model developed by Gibson et al. (2008b, 2009). The model, described in Appendix 1, follows the general theory developed by Fournier and Archibald (1982) and Deriso et al. (1985) for statistical catch-at-age models for stock assessment that allows auxiliary data to be incorporated for model fitting. This approach was adapted to use with several abundance life-stage specific indices (auxiliary data) to derive estimates of the age- and stage-specific abundances and survival rates required to analyze the dynamics of these populations. This information is then used to determine how recovery actions may be expected to change population size and viability.

The population dynamics model consists of two parts: a freshwater production model that provides estimates of the expected smolt production as a function of egg deposition and an eggper-smolt (EPS) model that provides estimates of the rate at which smolts produce eggs throughout their lives. These components are combined via an equilibrium analysis that provides estimates of the abundance at which the population would stabilize if the input parameters remained unchanged. This combined model is then used to evaluate how equilibrium population size has changed through time, as well as how the population would be expected to change in response to changes in carrying capacity, survival, or life stage transition probabilities, as described in Section 2.4.

There are two Atlantic Salmon populations in the Outer Bay of Fundy Designatable Unit with sufficient data for estimating values for life history parameters (i.e. with enough data that the above modeling approach can be used). These are the Nashwaak River and the Tobique River populations. The dynamics of the Tobique River population were analyzed by Gibson et al. 2009), the results of which are summarized here. The model equations, symbolism and statistical considerations for the model used for the Nashwaak River population are described in Appendix 1, and the population specific details of the modeling, model diagnostics and sensitivity analyses are provided in Appendix 2. The results of the analyses are summarized in the text below. For the Nashwaak River population, the model is set up using data from 1970 to 2011, whereas the analysis for the Tobique River population was fit to data for the years 1989 to 2005 (Gibson et al. 2009). Although this analysis was not updated here, preliminary analyses including more recent data provided estimates not dissimilar to those of Gibson et al. (2009).

Nashwaak River Population

The model results summarized in this section are for the base model run described in Appendix 1. Sensitivity analyses are provided in Appendix 2 and a comparison of the various model runs is provided in Appendix 2: Table A2.8.

Parameter estimates obtained for the Nashwaak River population are biologically plausible (e.g. mortality estimates between 0 and 1) and the standard errors of the estimates were not large relative to the means indicating reasonable model fits (Table 2.1, Appendix 2: Table A2.8). Mortality from the egg to the fry stages (at the time of the electrofishing surveys in mid summer) was estimated to be 0.96, meaning 96% of individuals die from the time of egg deposition to the time of the survey. The α parameter is the maximum survival from the fry stage to the age-1 parr stage, which occurs at low abundance in the absence of density dependence. The value of 0.54 means that, at most, an average of 54% of fry survive to age-1 (during the time period between the electrofishing surveys in one year and the surveys in the next). The carrying capacity of age-1 parr, R_{asy} , was estimated to be 28.0 parr per 100 m². This is the maximum density of age-1 parr that would occur if there were a very large (infinite) number of spawners in the river. The parameter value for j_2 of 0.61 is interpreted to mean that on average, 61% of the

age-2 parr undergo smoltification in the spring at that age and emigrate from the river. The value of j_3 is interpreted to mean that on average, 99% of the parr that remain alive in the cohort, undergo smoltification at age-3. The estimate of the annual mortality rate for parr older than age-1, M_{parr} , is estimated to be 0.53. This parameter is the proportion of parr older than age-1 that die annually (i.e. the mortality rate between age-1 and age-2, or between age-2 and age-3) and is assumed to be the same for all age classes in this category.

As described in Appendix 1, these parameter values can be combined to summarize the dynamics of juvenile salmon in freshwater (i.e. to describe survival from egg deposition to smoltification). The analyses indicate that the maximum number of smolts produced per egg is 0.007 (Table 2.1). This value is low relative to that seen in many other rivers (see discussion). The carrying capacity for smolt was estimated to be slightly more than 104,000 smolt. Again, these values can loosely be interpreted as averages for the time. Similar to the interpretation for parr above, the maximum number of smolts produced per egg occurs at very low abundance in the absence of density dependence and as abundance increases, survival decreases, resulting in a lower number of smolt per egg. The carrying capacity for smolt is the maximum number of smolt that would occur if there were a very large (infinite) number of spawners in the river.

The model is set up to provide estimates of the abundance of salmon at several life stages. In the case of the egg depositions, there are empirical estimates of egg depositions (calculated from adult escapement) and the model is fit to these data. In the case of the Nashwaak population, the model fits the data well (Figure 2.1). The time series do not show an increase in the egg depositions in the mid-1980's when the commercial salmon fisheries in the region were closed. Smolt abundance estimates from monitoring data are available from 1998 to 2011 (Figure 2.1) and the model is fit to these data as well. A nice feature of the model is that it can be used to estimate what the smolt abundances would have been over the entire time period. Based on these estimates, smolt abundance in the 1970's and 1980's would have been roughly two to five times higher than at present. The Nashwaak River contains about 53,505 habitat units (1 unit = 100 m^2 of habitat) upstream of the counting fence and smolt enumeration site (Jones et al. 2014). If these abundance estimates are scaled by amount of habitat in the river, they indicate that smolt production per unit area has decreased from a maximum of nearly 0.94 smolts per 100 m² to an average of 0.25 smolts per 100 m² during the last 10 years. These values are low relative to those seen in other rivers, but alone are not necessarily indicative of poor habitat quality. Rather, adult abundance in the Nashwaak River was never high enough during this time period to fully realize the production potential in the river (See Section 2.4). However, the very low maximum survival rate from egg to smolt (0.007) could be considered indicative of poor habitat quality.

Because the model is set up to produce estimates of smolt abundance in the past, and because adult counts are also available, return rates (both to the mouth of the river and to spawning escapement) can be estimated. This comparison of past and present return rates would not be possible without the model. The observed and estimated return rates of 1SW and 2SW salmon to the river mouth are shown in Figure 2.2. Both the 1SW and 2SW return rates show decreasing trends during the 1970's to the mid-1980's and increasing trends during the 2000's.

A summary (mean, minimum and maximum) of the return rate estimates for the 1973-82 and 2000-09 time periods is provided in Table 2.2. In the early period, return rates varied between 3.02% and 12.14% for 1SW salmon and between 1.30% and 9.07% for 2SW salmon. In the 2000's, return rates varied between 1.38% and 11.48% for 1SW salmon and between 0.41% and 1.96% for 2SW salmon. Return rates through to spawning escapement are also provided in Table 2.2. The difference in the return rates to the river mouth and to spawning escapement is the effect of the recreational fishery. In the earlier period, the fishery reduced the 1SW and

MSW returns to 63% and 68% of those to the river. In the 2000's, there is no effect because the fishery has been closed.

Bayesian posterior probability densities (Figure 2.3) indicate that the mean return rates for the two time periods are reasonably well estimated by the model, and 95% Bayesian credible intervals (an indicator of the probability that the rates are different) for 2SW return rates do not overlap. The difference in the return rates between the two time periods for 1SW salmon is less than for 2SW salmon.

Tobique River Population

The results presented here are a summary of the analyses by Gibson et al. (2009) for the Tobique River population using data from 1989 to 2005. The freshwater model parameters have the same interpretation as for the Nashwaak River population. Comparing the freshwater dynamics between these two populations: the proportion of age-2 smolts in a cohort, the carrying capacity for parr, and the survival of older parr are estimated to be lower in the Tobique than in the Nashwaak; but the maximum survival rate from age-0 to age-1 is estimated to be higher (Table 2.1).

Based on the analyses of Gibson et al. (2009), under recent conditions the maximum number of smolts produced per egg ($\breve{\alpha}$) was estimated to be 0.0046 with an asymptotic population size (\breve{R}_{asy}) of 27,009 smolts. Both these estimates are quite low, the latter equating to 0.34 smolts per 100 m². For comparison, 3.8 smolts per 100 m², calculated for Atlantic Salmon in the 1970's (Symons 1979) is sometimes used as a general reference value.

The model for the Tobique River population was not set up to estimate return rates because the effects of the Mactaquac program (broodstock removals, trapping and trucking) make it impossible (with the current) to determine which salmon were destined for which tributary upstream of Mactaquac Dam. For this reason, Gibson et al. (2009) used the return rates to the Nashwaak River as a proxy for those to the Tobique River when analysing the dynamics of the Tobique River salmon population. An important difference between these populations is that mortality of salmon migrating downstream through head ponds and past turbines is thought to be 45.3%. All other things being equal, this would reduce return rates to the Tobique River to just over one half those to the Nashwaak River.

2.3 MORTALITY OF ADULT SALMON BETWEEN SPAWNING EVENTS

Estimates of the proportion of salmon in the Nashwaak River that return to spawn for a second or a third time are provided in Appendix 2 (Table A2.4) based on cohorts spawning for the first time during the 1993 to 2009 time period. Within the 1SW component, alternate-year repeat spawning is more common, whereas the rates of repeat spawning using an alternate-year or a consecutive-year strategy are similar for 2SW salmon. Overall, 3.1% of 1SW salmon and 9.0% of 2SW salmon return to spawn for a second time. Within the 1SW component, all salmon returning to spawn for a third time are returning the year after their second spawning, whereas in the 2SW component, a greater proportion skip a year between their second and third spawning. Return rates between the second and third spawning averaged 18.0% and 39.2% for salmon originally spawning as 1SW and 2SW salmon, respectively.

2.4 POPULATION DYNAMICS: PAST AND PRESENT

Gibson and Bowlby (2013) describe the use of equilibrium analyses in evaluating the effects of human activities or natural perturbations on salmon populations as follows (figure numbers are edited to match this document):

"Human activities may affect some parts of a fish population's life history, such as its average fecundity, survival from one age class or life stage to the next, age-at-maturity or the number of times an individual reproduces. These parameters in turn affect the population's productivity, and one way to assess the effects of a human activity is to evaluate the expected change in productivity that results from changes in life history parameters.

Equilibrium modeling is one approach that can be used to assess impacts of human activities in this way. This kind of analysis begins by splitting the life cycle of salmon into two parts, and for a given set of life history parameters, determining the population size at which the rates in each part of the life cycle are balanced such that the population does not increase or decrease in size. This is the population equilibrium for that specific set of parameter values. By varying the life history parameters in a manner that represents the expected response to a human activity and examining the resulting change in equilibrium population size, the effects of the activity on the population dynamics (Moussalli and Hilborn 1986), for estimating biological reference points for fisheries management (Myers et al. 1994), for providing a basis for the estimation of the long-term consequences of mortality caused by pollution, dams or other human activities (Barnthouse et al. 1988) and for linking fish habitat and fish population dynamics (Hayes et al. 1996).

In the case of Atlantic Salmon, a natural split in the life cycle occurs at the smolt stage when fish are migrating to the marine environment. The first part of the model gives freshwater production (the number of smolt produced as a function of egg deposition). The second part is the lifetime egg-per-smolt relationship, which gives the rate at which smolts are expected to produce eggs during their entire life. This approach is illustrated in Figure 2.4. In this example, the commonly used Beverton-Holt function is used to model smolt production in fresh water (Figure 2.4a). This model has two parameters: the slope of the function at the origin which gives the maximum rate at which eggs survive to become smolts. This is based on the idea that survival is greatest when population sizes are very low because competition between fish, which can result in reduced growth and increased mortality, is low. The other parameter is the carrying capacity of the river, which is the number of smolts that would be produced if egg deposition was extremely high. Changes in habitat quantity, say as a result of providing fish passage to areas that were previously inaccessible, have the effect of changing carrying capacity. Changes in habitat guality, say as a result of improving or reducing water quality, has the effect of changing the slope at the origin, but may also change carrying capacity as well (Hayes et al. 1996). Although only two parameters are used here, they combine the effects of egg-to-fry survival, fry-to-parr survival, parr-to-smolt survival and age-at-smoltification (Trzcinski et al. 2004).

The lifetime egg-per-smolt (EPS) relationship (Figure 2.4b) is assumed to be density independent. This is to say that the rate at which smolts produce eggs throughout their lives does not depend on the number of smolts that are produced. This is the equivalent of assuming resource availability in the marine environment is not limiting population growth, and therefore mortality at sea is not density-dependent. In contrast, resource availability in freshwater (see above), which determines carrying capacity, was assumed to limit production of smolt. This paradigm is consistent with most population models for diadromous fish, and is further supported by a recent analysis of the timing of density dependence in Atlantic Salmon, which found strong evidence for density dependence in salmon populations within fresh water and little evidence for

density dependence in salmon within the marine environment (Gibson 2006). The rate at which smolts produce eggs is calculated based on the survival of juvenile salmon in the marine environment, age-at-maturity, fishing mortality, fecundity, and the number of times a fish spawns throughout its life.

The population equilibrium is derived by finding the abundance at which the production of smolts by eggs equals the reciprocal of the production of eggs by smolts (Figure 2.4c); note that graphically this is the equivalent of flipping the axes in Figure 2.4b, so that the plots can be overlain. The equilibrium is the population size at which the population will stabilize if all model parameters do not change. Effects of human activities or other changes to population dynamics are evaluated by examining how the equilibrium changes in response to changes in the life history parameters resulting from the activity. In the example shown in Figure 2.4c, a decrease in smolt-to-adult survival shifts the equilibrium point to a smaller population size goes to zero and the population will become extinct in the absence of human intervention or a change in one or more of the vital rates. However, an equilibrium population size greater than zero does not necessarily mean that a population is viable, because no allowance is made for random variability in the life history parameters or for catastrophic events."

The mathematics underlying the equilibrium analysis, including the EPS calculations and the calculations for equilibrium population size, are provided in Appendix 1.

The lifetime egg-per-smolt models are a useful mechanism for evaluating how the changes in return rates described in Section 2.2 influence a smolt's contribution to subsequent salmon production. The results of these analyses for the Nashwaak population are summarized in Table 2.3. For this population, EPS values ranged between 117 and 732 eggs/smolt in the 1973-82 time period, and between 49 and 151 eggs/smolt in the 2000's. Similar to the return rate analyses, the difference in the values calculated using return rates to the river mouth and to spawning escapement is an indicator of the effects of the recreational fishery. In this case, EPS at spawning escapement was reduced to 65% its value at the river mouth during the early time period. Bayesian posterior probability densities for the aveage lifetime egg-per-smolt estimates for the two time periods (Figure 2.5) indicate that the maximum likelihood estimates reasonably match the modes of the posterior densities. The 95% Bayesian credible intervals for the two time periods do not overlap for either population (an indicator of the probability that the rates are different).

Gibson et al. (2009) estimated that the EPS value for the Tobique River population (using 1989 to 2005 data) was 38.5 eggs/smolt, a value which is low. Given their freshwater production estimate described above, one smolt would have to produce more than 217 eggs (the inverse of 0.0046 smolts per egg) in order for the population to replace itself.

The results of the equilibrium analyses for the Nashwaak River salmon population are summarized in Table 2.4 and Figure 2.6. As mentioned, the equilibrium is the population size at which the population will stabilize if all model parameters do not change. To see how this works, consider Figure 2.6, top panel. Start at an egg deposition of 5 million eggs, and use the curved freshwater production line to determine how many smolts would be produced (slightly over 20,000 smolts). Then use the average EPS line (the middle dashed line) to determine how many eggs would be produced by that number of smolts (in the vicinity of 9 to 10 million eggs). Then, for that number of eggs, determine how many smolts would be produced, and so on. One should rapidly approach the equilibrium (the point where the freshwater production curve intersects the EPS line). Then try the same thing in Figure 2.6, bottom panel, starting at 20 million eggs. It should become evident that the equilibrium is an attractor towards which the

population moves, and that recovery planning is about shifting the attractor to a place that causes the population to increase in size.

As shown in Figure 2.6, the equilibrium population size for the Nashwaak River population varied substantially in the 1970's and early 1980's because of the variability in the return rates during that time period. At the minimum return rates observed during that time period, the equilibrium population size was zero. During the 2000's, the mean equilibrium for the Nashwaak River population was 1.7 million eggs (Table 2.4), Although this value is greater than zero, but is low enough that the population is expected to be at risk of extirpation due to the effects of random environmental variability, as shown in the next section. The maximum lifetime reproductive rate for the Nashwaak population (Table 2.4, Figure 2.7) has decreased from averages of 2.49 in the 1973-82 time period, to an average of 1.13 during the 2000's. These values mean that during the 2000's, at low abundance and in the absence of density dependence (which further lowers reproductive rates), a salmon in the Nashwaak River produces on average a total of 1.13 replacement salmon throughout its life, indicating that the population has almost no capacity to rebuild if environmental events such as floods or droughts lower survival at some point in time. Note that the minimum rate indicates that there are years of low survival, which is why this population is at risk from environmental stochasticity.

Table 2.4 also provides a comparison of the equilibrium population size of the Nashwaak River population with and without the recreational fishery in the past. This metric is better for evaluating the effects of the fishery than the return rate and EPS comparisons presented earlier, because in addition to showing how egg production is decreased, the equilibrium analyses also take into account the capacity of the population to compensate for this reduction. In the case of the Nashwaak River population, this capacity is not high due to the low freshwater productivity already described. Although the recreational fishery had the effect of reducing the lifetime egg production per smolt to about 65% of its value without the fishery, its effect on the average equilibrium egg deposition was to reduce it to 40% its value without the fishery. Similarly, the maximum lifetime reproductive rate was reduced from an average of 2.49 to 1.60, reducing the population's resiliency to low survival events.

Gibson et al. (2009) conducted an equilibrium analysis for the Tobique River population to examine the combined effects of low freshwater productivity, downstream passage mortality for smolts and low at-sea survival. They used the following scenarios to explore the scope for management to facilitate recovery and to model the potential outcomes of future management strategies:

- 1. increased at-sea survival for immature salmon,
- 2. increased survival for migrating smolts (intended to represent improvements to downstream fish passage at all three hydroelectric facilities), and
- 3. increased freshwater productivity, resulting in greater smolt production within the river (intended to represent freshwater habitat restoration activities).

For scenario 1, they compared three levels of at-sea survival:

- 1. the current state using the mean return rates for salmon in the Nashwaak River (3.2% for 1SW and 0.9% for 2SW),
- the most beneficial observed state on the St. John River system (6.4% for 1SW and 1.6% for 2SW), and
- 3. a hypothetical reduction in at-sea mortality, in which return rates for 1SW and 2SW fish were assumed to equal 8% and 3%, respectively.

For scenario 2, they evaluated the effect of increasing survival of emigrating smolts by comparing two levels of passage survival:

- 1. the status quo in which fish passage survival of smolt is 54.7%, and
- 2. a hypothetical scenario in which passage survival of smolt was increased to 100%.

These values were thought to bracket the range of possible outcomes to improved fish passage. For scenario 3, they explored two levels of freshwater productivity to examine its importance on equilibrium population size. The first represented present conditions and used the parameter values determined from the freshwater production model (Table 2.1). The second was a hypothetical situation in which the asymptotic recruitment level and maximum survival rate of age 1 parr were doubled, such that $M_{parr} = 0.49$ and $R_{asy} = 18.6$. Gibson et al. (2009) describe their results as follows (figure and table numbers are changed to match this document):

"Under present freshwater conditions in the Tobique River, the maximum number of smolts produced per egg ($\breve{\alpha}$) was estimated to be 0.0046 with an asymptotic population size (\breve{R}_{asy}) of 27,009 smolts. This latter estimate is quite low, equating to 0.34 smolts per 100 m² (using the habitat area estimate obtained from orthophoto maps). For comparison, 3.8 smolts per 100 m², calculated for Atlantic Salmon in the 1970's (Symons 1979) is sometimes used as a general reference value. The low production estimate for smolt in the Tobique is surprising given past salmon abundance in this river. Under the hypothetical scenario of improved freshwater production, the maximum number of smolts produced per egg ($\breve{\alpha}$) is 0.012 with an asymptotic population size (\breve{R}_{asy}) of 141,733 smolts. This value is equivalent to 6.53 smolts per 100 m² of habitat.

At the average observed smolt-to-adult return rates, but at a hypothetical fish passage survival rate of 1.0, lifetime egg production per smolt was calculated to be 77 eggs. Presently, the estimated passage survival rate of Tobique River Atlantic Salmon is 0.547 (AMEC 2005; Carr 2001), which reduces the expected lifetime egg production of a smolt to 38.5 eggs. Given current freshwater production estimated above, one smolt would have to produce more than 217 eggs (the inverse of 0.0046 smolts per egg) throughout its lifetime in order to have an equilibrium population size greater than zero. As such, the population would be expected to decline to extinction in the absence of human intervention or a change in the vital rates.

Consistent with the above values, the scenario analyses (Table 2.5, Figure 2.8) indicate that addressing fish passage mortality alone, with no change in either freshwater production or survival at-sea, is not expected to be sufficient to create a viable population. Similarly, if treated in isolation, increasing marine survival rates to 6.4% and 1.6% for 1SW and 2SW fish, respectively, or even to 8% and 3%, does not result in an equilibrium population size greater than 0 (Figure 2.8, top panel). Similarly, the population equilibrium remains at zero if only the capacity of the freshwater environment to produce smolts is increased (Figure 2.8, top panel). However, a small equilibrium population size exists if fish passage and freshwater production are increased concurrently and at-sea survival remains at its average level (Figure 2.8, lower panel). This equilibrium is well below the conservation requirement for this population (Table 2.5).

Equilibrium population sizes that were very close to or above the conservation requirements for the Tobique River could be produced under three scenarios: (1) when

freshwater production was improved and marine survival was increased to the highest modeled value and fish passage was at current levels (Table 2.5), (2) when freshwater production and fish passage were increased and marine survival was equal to the highest observed values in the Nashwaak River (Table 2.5), and (3) when fish passage survival and freshwater production were increased and at-sea survival was equal to 8% and 3% for 1SW and 2SW Atlantic Salmon, respectively (Table 2.5). The effect of at-sea survival on egg deposition is evident in Figure 2.8: under the improved freshwater production scenario, increasing at-sea survival from the maximum observed rate to the maximum hypothetical rate nearly doubles the equilibrium egg deposition with only a small increase in smolt production. Taken together, these scenarios show that although improvements to fish passage seem to have little influence on the equilibrium size of the population given current levels of freshwater production and at-sea survival, low fish passage survival does have the potential to limit the effectiveness of recovery actions focused on other life stages."

3.0 POPULATION VIABILITY ANALYSIS USING PRESENT LIFE HISTORY PARAMETERS

The long term population projections are carried out using a population viability analysis (PVA) following the approach of Gibson and Bowlby (2013) for Southern Upland Atlantic Salmon. They describe the role of PVA in conservation biology as follows:

"PVAs are used extensively in conservation biology to predict both the risk of extinction for populations and species and to evaluate management strategies to recover at-risk populations. In a PVA, a population dynamics model is used to determine how the probability of persistence is affected by current conditions and future perturbations (Beissinger and McCullough 2002), and models are often used to identify threats to the persistence of a population and to evaluate how future management actions or environmental changes may influence the probabilities of extinction or of achieving recovery goals (Reed et al. 2002). Using simulations of population trajectories, PVA allows one to explore the logical implications of current knowledge and assumptions (Bowlby and Gibson 2011).

Although some authors have cautioned against the use of PVAs because the predictions, typically time to extinction, are almost always quite uncertain (e.g. Taylor 1995; McCarthy et al. 1996; Ludwig 1999), many authors believe that PVA's can be used to assess relative risk (e.g. Akçakaya and Raphael 1998; Beissinger and Westphal 1998; McCarthy et al. 2001). Reed et al. (2002), argue that these relative evaluations are the most appropriate use of PVAs and can be used as a basis for choosing the most effective management strategy from a given set of possibilities (Lindenmayer and Possingham 1996).

Some relatively simple PVA models are possible. For example, the Dennis-type PVA (Dennis et al. 1991) can be used to evaluate extinction risk if the assumption is made that future trends will be similar to past trends, although this type of model is of limited utility for evaluating recovery actions because the underlying biology is not considered. Models which track abundance at multiple life stages are therefore preferred when evaluating population persistence (O'Grady et al. 2004), provided adequate data are available and uncertainties are accounted for (Holt and Peterman 2008, Legault 2005, McCarthy et al. 2001). [text deleted]

With respect to selecting recovery strategies, McCarthy et al. (2003) used a simulation study and found that they were able to identify the better of two management

strategies 67-74% of the time using 10 years of data, and 92-93% of the time with 100 years of data."

The PVA model used here is described in detail in Appendix 3. It is an adaptation of the population dynamics model used to estimate life history parameter values (described in Appendix 1), and is also adapted from the PVA model developed by Gibson and Bowlby (2013) to reflect differences in the available information about repeat spawning dynamics between the LaHave River population and the Nashwaak River population (also described in Appendix 1). The model is fully age- and stage-structured and tracks abundance of all life stages and age classes for the duration of the forward projection. As described in Appendix 3, auto-correlated random variability is added at each age class or life stage transition. As the strength of this autocorrelation increases, good years are increasingly likely to be followed by good years (and bad followed by bad). Here the same autocorrelation and variances were used as were used by Gibson and Bowlby (2013) for the Southern Upland populations.

As was done by Gibson and Bowlby (2013), two versions of the PVA were run in parallel using values for two time periods: the past (the 1973-1982 time period) and the present (2000 to 2009) when the dynamics of the populations were very different. Comparison of the PVA results from these periods helps to ensure that the conclusions about present population viability are not simply a modeling artifact in the PVA.

Similar to Gibson and Bowlby (2013) extreme environmental events were included in the PVA:

"Additionally, because Atlantic Salmon occupy habitats that are periodically subject to extreme conditions (e.g. floods and droughts), the effects of extreme events (which can lead to very high mortality) were included in the model. The life history of Atlantic Salmon, which distributes the reproductive effort of a cohort over multiple years, likely evolved in part as a strategy to cope with this kind of variability, and changes in their dynamics can affect the age structure in a population. In this analysis, extreme events affect survival between the egg and the fry life stages, thereby allowing density-dependent compensation to occur which would partially offset some of the mortality. The effect of the extreme events would be greater if it was incorporated after density dependence (i.e. after age 1) in the life cycle.

The frequency and magnitude of extreme environmental events has not been determined for these populations. In most model runs, the probability that an extreme event occurred was set to 0.1 and the effect of the extreme event was assumed to reduce fry abundance by 80%. This means that on average, 10 events reducing the abundance of fry by 80% from the expected value would occur every 100 years. As modeled, a greater or lesser number of extreme events could occur in any simulated population trajectory, and their distribution through time is random (see Appendix 3 for details). The sensitivity of the results to these assumed values was evaluated by running scenarios with no extreme events as well as scenarios with more extreme environmental events. As shown in Section 2, the population growth rates of Outer Bay of Fundy Atlantic Salmon are currently very low, making it difficult for populations to recover after low survival events. Although the values used to simulate extreme mortality events are assumed, this loss of resiliency is illustrated via this analysis."

The rationale for including extreme environmental events in the PVA for the Nashwaak population is the same.

Analyses were carried out for Nashwaak River salmon populations using both the "past" and "present" dynamics. The population is modeled as a closed population, meaning that it is not affected by either immigration or emigration.

Gibson and Bowlby (2013) further describe the model:

"For each scenario analyzed with the PVA, 2000 population trajectories were simulated and the extinction and recovery probabilities were calculated as the proportion of populations that go extinct by a specified time. For both the past and present scenarios, the population was projected forward from a starting abundance based on the estimated adult population size in 2010. The population was assumed to be at equilibrium, and the numbers of eggs, parr, smolt and adults, as well as their age, sex and previous spawning structure, at the start of each simulation were calculated from the adult abundance using the life history parameter values specific to the dynamics being simulated. To evaluate extinction probabilities, a quasi-extinction threshold of 15 females was assumed. This means that annual egg deposition is given a value of zero if the abundance drops below 15 females. A population must be below this value for two consecutive years to be assumed extinct in a given year. However, if the female abundance is higher in the next year, the egg deposition is calculated as per the model. A population can therefore sit on the quasi-extinction threshold for a number of years and can theoretically recover unless there are several sequential years where the female spawner abundance is less than 15. When evaluating recovery probabilities, the conservation requirement was used as the recovery target. The probability of recovery is calculated as the proportion of the simulated populations that are above the recovery target in a given year. Abundance in a population may be above the recovery target for a period of time, but is no longer considered recovered if its abundance subsequently drops to a level below the recovery target.

Abundances for each life stage were projected forward for 100 years even though there is considerable uncertainty about what the dynamics of these populations will be at that time. However, the reason for using these long term projections is not to estimate what abundance will be at some time, but rather to evaluate longer term viability for each scenario (i.e. does the projection go to zero or not). In other words, the longer term projections are used to determine whether the populations are viable for each combination of life history parameters, random variability and extreme events included in the scenario."

3.1 POPULATION VIABILITY IN THE PAST AND AT PRESENT

Abundance trajectories for the Nashwaak River salmon population (Figure 3.1) indicate that, given the present (2000's) population dynamics, this population is expected to decline towards extirpation and has zero probability of reaching its recovery target (Table 3.1, Figure 3.2). The probability of extirpation (Table 3.1, Figure 3.2) increases after about 40 years, with 28% of the simulated populations being extirpated within 100 years. None of the 2000 simulated population trajectories met the recovery target within 100 years (Table 3.1). In contrast, abundance trajectories using the past (1973-82) dynamics (Figure 3.1) indicate rapid population growth. None of the simulated population trajectories extirpate within 100 years (Table 3.1, Figure 3.2), but only abount 55% of the simulated populations are above the recovery target, in any given year, 50 years in the future.

3.2 EFFECTS OF EXTREME ENVIRONMENTAL EVENTS

The effects of environmental variability and extreme events were investigated using the Nashwaak River population model. For each scenario described below, 2000 simulated population trajectories were run, each starting at the 2008-2012 average adult abundance. The Nashwaak River population has an equilibrium population size greater than zero, and therefore would not become extinct in the absence of environmental variability, as shown by the deterministic model in Figure 3.3 (top left panel) (refer also to Section 2.4). However, when random variability is added to the projections (using the same life history parameter values as in the base model), populations begin to become extinct towards the end of the simulations (Figure 3.3 – left column, second panel from the top). When extreme events are added, extinction risk increases further (Figure 3.3 – left column, third panel from the top). Changing the frequency and magnitude of the extreme events changes the extinction probabilities as expected (Figure 3.3 – left column, bottom two panels). However, when the same random variability and extreme event scenarios are modeled using the 1973-1982 dynamics, none of the 10,000 simulated population trajectories become extinct. This highlights the resiliency that these salmon populations had in the past to environmental variability as a result of higher maximum lifetime reproductive rates.

3.3 EFFECT OF TIME (STARTING POPULATION SIZE)

The analyses indicate that in the absence of human intervention or a change in survival for some other reason, abundance of these two Outer Bay of Fundy populations salmon will continue to decline. To examine the effect of delaying recovery activities, the population viability analysis (base model) for the Nashwaak River population was re-ran starting at 100%, 50%, 25% and 10% of the 2008-2012 mean abundance estimates used in the base model simulations (896 small salmon and 263 large salmon). Using the present dynamics, further reductions in population size have the effect of shortening time to extinction (Figures 3.4 and 3.5). A reduction in starting populations have not extirpated within the 100 year time period, whereas a reduction in size of 75% reduces the time to which 50% of the simulated populations are extinct to about 90 years. Using the 1973-1982 dynamics, time to recovery is similarly increased (Figures 3.4 and 3.5). When the analysis is run using the 2012 abundance (29 small salmon and 63 large salmon) using the 2000's dynamics, the extinction risk is much higher, about 25% in 50 years.

3.4 SENSITIVITY TO THE QUASI-EXTINCTION THRESHOLD

The results presented in this section are derived using a quasi-extinction threshold of 15 female salmon. Population viability analyses are known to be sensitive to the assumed threshold. This value is very low relative to the past abundances of salmon in these rivers. If depensatory dynamics exist, populations may not be able to recover from low abundances, even ones that are higher than this threshold. To evaluate the effects of the assumed quasi-extinction threshold on the estimated extinction probabilities, the analysis using the Nashwaak River population model was re-ran with the quasi-extinction threshold increased to 30, 50 and 100 female salmon (values that are still very low relative to past abundance). When scenarios are run using the 2000's dynamics, time to extinction decreases markedly as the threshold is increased (Figure 3.6). However, this threshold has nearly no effect on rebuilding times when the 1973-1982 dynamics are used.

4.0 POPULATION VIABILITY ANALYSIS OF RECOVERY AND ALLOWABLE HARM SCENARIOS

4.1 RECOVERY SCENARIOS

To evaluate how the probability of extinction and probability of meeting the recovery target would be expected to vary with increased freshwater productivity and increased lifetime egg production per smolt, 24 scenarios were evaluated using the Nashwaak River population PVA model. Information about the nature and magnitude of recovery actions required for the recovery actions for the Tobique River salmon populations was provided in Section 2.4.

The values used in the EPS component of the model were derived using the 1973-19822 and 2000-2009 parameter values (fecundity, return rates and sex ratio) as upper and lower estimates, respectively (Table 4.1), with two intermediate scenarios evenly spaced between these (i.e. at 1/3rd and 2/3rd the difference between past and present values).

Increased freshwater production was modeled by increasing smolt production by factors of 1.0 (no increase), 1.2 (20% increase), 1.5 (50% increase) and 2.0 (double or 100% increase).

Each combination of increased freshwater productivity and at-sea survival was modeled for a total of 16 scenarios (see results below). In addition, eight other scenarios are presented to investigate the effects of extreme events. In these, freshwater productivity was increased by a factor of 1.5 and simulations were carried out for all four at-sea survival values. For each scenario, the probabilities of extinction and recovery were evaluated using 2000 simulated population trajectories.

Abundance trajectories, extinction probabilities and recovery probabilities for the Nashwaak River population for each scenario are provided in Figures 4.1, 4.2 and 4.3, respectively. Associated numerical values are provided in Tables 4.2. The results of these analyses indicate how close the Nashwaak River Atlantic Salmon are to the threshold between becoming extirpated and being viable. Panel "A" in each figure shows the results using the current dynamics; as previously described, the population is expected to extirpate in the absence of human intervention or a change in vital rates for some other reason. Panel "B" shows the effect of increasing freshwater productivity by 20%. This improvement is not large, but does markedly reduce extinction risk, even if marine mortality rates remain unchanged. None of the 2000 simulated populations became extinct within 100 years under this scenario. Similarly, relatively small changes to the marine component of the model lead to viable populations; none of the simulated populations extirpated in the 1/3rd increase scenarios (Panel G) and a small proportion of the populations reached their recovery targets. Although small, numerically-viable populations are produced in both of these examples, greater changes are necessary in order for populations to consistently be above their conservation requirements, and likely require both a change in freshwater productivity and in lifetime production of eggs by smolts, as shown by the increase in proportion reaching the recovery target as freshwater productivity increases (Figure 4.3; compare Panels G to J). Additionally, a recovery probability of 84% in 30 years is achieved in the 2/3rd increase in the marine component when combined with a freshwater productivity increase of 50% (Panel O). In contrast, increases in the EPS component to the past levels without an increase in freshwater productivity only produce an 8% probability of meeting the recovery target (Panel M). Within limits, these conclusions are robust to how the frequency of extreme events is modeled (Panels E, K, Q, W, F, L, R, X). The probability of recovery increases when the frequency of the extreme events is reduced (e.g. compare Panels R and O).

4.2 ALLOWABLE HARM SCENARIOS

The effects of increased levels of harm to the population were also evaluated using the PVA for the Nashwaak River population. Here, decreased freshwater production was modeled by decreasing smolt production by factors of 1 (no decrease), 0.9 (10% decrease), 0.8 (20% decrease), 0.7 (30% decrease) and 0.5 (50% decrease). Decreases in at-sea survival were modeled as decreases of 0%, 10%, 30% and 50%. Extinction probabilities for each scenario are shown in Figure 4.4 and the associated numerical values are provided in Table 4.3.

None of the simulated populations recovered in these scenarios and extinction probability increased rapidly with relatively low levels of harms. For example, the 10% decrease in either at-sea survival or freshwater productivity increased the 100 year extinction probability to about 80%. Although under these scenarios the extinction risk is low on the time scale of a couple decades (Table 4.3), this result is because of the starting population size. The population would be in decline over the entire time period, and the use of a lower starting population size would decrease the time to extinction.

5.0 DISCUSSION, UNCERTAINTIES AND CONCLUSIONS

The dynamics of two Outer Bay of Fundy Atlantic Salmon populations were analyzed: the Tobique River population (thought to be representative of populations upstream of Mactaquac Dam) and the Nashwaak River population (thought to be representative of populations in the Saint John River downstream of Mactaquac Dam). A major difference in the present dynamics between these populations is the effect of hydroelectric development on the upstream populations. One of the effects of this development is a reduction in the smolt-to-adult return rates by 45.7% as a result of reduced survival of downstream migrating smolts. As such, extinction risk for populations above Mactaquac Dam is much higher than for those populations downstream.

In order to carry out the recovery scenario analyses, a decision had to be made about whether to only vary at-sea survival, or whether to also vary the sex ratio and fecundity values. As shown in Table 4.1, one of the changes is a near doubling of the proportion female in the 1SW component of the population. Assuming there is a genetic component to age-at-maturity, this could be the result of either genetic drift, or due to selective pressure as a result of increased at-sea mortality. If the former, then in the recovery scenarios, modeling changes in at-sea survival only would be appropriate, whereas if the change is due to selective pressure, then having the sex ratios revert back in the increased at-sea survival scenarios would be appropriate, as was done. Preliminary analyses (not shown) indicated that if the decision was made not to allow the sex ratios to change, extinction risk would be slightly lower than as modeled with the sex ratio change.

Although population projections were not done for the Tobique River population, the allowable harm analysis for the Nashwaak may be partially informative with respect to the effect of hydroelectric development on the populations. As already shown, the equilibrium population size under current conditions for this population is zero and the population is expected to extirpate in the absence of human intervention or a change in survival for some other reason. If all other factors were the same (starting population size, all life history parameters), a comparison of scenario A and scenario E in Figure 4.4 could be considered to approximately show how extinction risk differs as a result of this development.

Although times to extinction and recovery are presented in this document, readers are cautioned not to interpret these values too literally, given that prediction of extinction times using PVA is known to be highly uncertain (Taylor 1995; McCarthy et al. 1996; Ludwig 1999). As

mentioned in the introduction to the PVA analyses, the most appropriate use of PVA's is to assess relative risk (e.g. Akçakaya and Raphael 1998; Beissinger and Westphal 1998; McCarthy et al. 2001) which can be used as a basis for choosing the most effective management strategy from a given set of possibilities (Lindenmayer and Possingham 1996). When comparing scenarios for Outer Bay of Fundy Atlantic Salmon, the important information is how much the time to extinction or recovery changes with when survival changes, not that extinction is predicted in (for example) 40 years.

The maximum survivals from egg to smolt (the slope at the origin of the spawner-recruit curve) for both populations (0.007 and 0.005 for the Nashwaak and Tobique populations, respectively) appear low relative to the values estimated for some populations, but not others. Using a similar model, Gibson and Bowlby (2013) estimated values of 0.017 and 0.034 for the LaHave River (above Morgans Falls) and the St. Mary's River (West Branch) populations, respectively, two populations thought to be partially effected by river acidification. In contrast, Gibson et al. (2008b) report a value of 0.005 for the Big Salmon River. O'Connell et al. (2006) compared egg to smolt survival for nine Atlantic Salmon populations in eastern Canada. The Nashwaak River population had the lowest survival in the comparison after adjusting for density dependent effects by standardizing by river size and egg deposition (their Figure 17).

The results presented here highlight some important differences between the dynamics Outer Bay of Fundy Atlantic Salmon and those of the Inner Bay of Fundy and Southern Upland. At-sea survival estimates for Outer Bay of Fundy salmon (as inferred by from the Nashwaak River population) are roughly ten times higher than those for Inner Bay of Fundy salmon (Gibson et al. 2008a). For the Inner Bay of Fundy populations, at-sea survival is low enough that it cannot be offset by recovery actions focused on other threats. Although at-sea survival of both Outer Bay of Fundy and Southern Upland Atlantic Salmon has decreased, it remains high enough that small increases in freshwater productivity are predicted to lead to small but viable populations, an outcome that is not possible within the Inner Bay. However, for both Outer Bay of Fundy and Southern Upland salmon, increases in at-sea survival will be needed if populations are to be recovered to abundances above their respective conservation requirements. Readers are cautioned that, because of the fundamental differences in the dynamics of salmon populations in the regions (both in fresh water and in the marine environment), extrapolating about the limiting effects of at-sea survival from one region to another could lead to erroneous conclusions about its overall effects on recovery potential and population viability. In addition, within the Outer Bay of Fundy designatable unit, extrapolation from populations below Mactaquac Dam to those found in tributaries above Mactaguac Dam requires a correction for the effects of reduced downstream survival.

Gibson and Bowlby (2013) provided the following guidance on interpreting the recovery targets and probability of recovery when describing the PVA for Southern Upland salmon:

"Throughout these analyses, the conservation requirement was used as the recovery target when assessing the probability of recovery, consistent with its definition when it was developed and its use as the critical-cautious boundary in the precautionary fisheries framework (see Bowlby et al. 2013a). In the analyses here, small increases in productivity and survival led to populations that were viable (conditional on model assumptions) at levels well below the conservation requirement. However, it is not known whether these populations would truly be viable in the longer term because the smaller populations may be at risk due to declining fitness caused by genetic effects, including inbreeding and loss of genetic variation (Frankham 2008).

Lande and Barrowclough (1987) showed that an effective population size (Ne) of approximately 500 individuals can maintain most genetic variability, although there are

estimates of the number required that are lower. For Atlantic salmon, Elliott and Reilly (2003) found that an effective breeding population of 80-90 individuals was sufficient to maintain most of the genetic variability in populations introduced in Australia and Tasmania. Census population sizes (Ncensus) would be expected to be larger. Although overlapping generations, iteroparity and straying make the estimatation of Ne difficult, there are several studies that have estimated Ne and Ne/Ncensus ratios for salmonids (reviewed in Trzcinski et al. 2004). The average of the lower and upper limits of Ne/Ncensus ratios across taxa and studies give a range from 0.26 to 0.88. If we use the range of 0.26-0.88 and assume that a minimum of 80-100 individuals are necessary to maintain genetic variability, then the minimum total population size should be between 91-385. If Lande and Barrowclough's (1987) more conservative estimate of a minimum effective population size of 500 individuals is used, then minimum census population size should be between 568-1,923 individuals. These values assume a closed population. If straying exists between rivers, the minimum census population size required to maintain genetic diversity would be lower."

As discussed in Jones et al. (2014), the recovery target should be revisited once populations are selected for recovery, recovery actions are identified, and information about the expected dynamics of the recovered population is obtained. In this document, the probability of recovery should be interpreted in the context of reaching the conservation requirement rather than in the context of preventing extinction. The sensitivity analyses with respect to the quasi-extinction threshold indicates how extinction risk increases if larger population sizes are required for longer term viability.

Overall, the retrospective examination of the recreational fishery on the Nashwaak River population indicated that the fisheries did reduce population size, and that this reduction was great enough to have been a contributing factor to the overall population decline: a 60% reduction in equilibrium egg depositions in the 1973-1982 time period when retention fishers were open for both large and small salmon. Although not shown here similar analysis for the 1980-1989 time period show a 53% reduction in the equilibrium egg deposition during a period when the transition to hook-and-release fisheries was occurring.

These analyses of the population dynamics are not adjusted for the effects of commercial fisheries, either locally in the past, or presently in international or distant waters. Without this adjustment, the effect is to underestimate maximum lifetime reproductive rates and hence viability. This effect would have been greater in the past when local commercial fisheries were operating and when landings in international and distant waters were higher, and as a result, the changes in the dynamics between the past and present scenarios may be underestimated, with higher levels of productivity in the past.

The population viability analyses illustrate the expected population trajectories for a specific set of life history parameter values, but do not include linkages among the various survival rates. For example, it has been suggested that survival of fish in large schools is enhanced when traveling through predator fields compared to fish traveling singly or in small schools (Cairns 2001). As another example, the age-of-smoltification may be linked to the growth rates of parr, which can be density dependent.

The information on population dynamics presented here indicate that abundance of Outer Bay of Fundy Atlantic Salmon is expected to continue to decline in the absence of human intervention or a change in life history parameters for some other reason. As shown by the population viability section (Section 4), both the probability of extinction and the time to recovery increase if abundance decreases further before recovery actions are initiated. For example, extinction risk in the nearer term was much higher when the 2012 abundance estimates were

used to initialize the population, which are much lower than the 5-year average used in most model runs. As was noted for Southern Upland salmon (Gibson and Bowlby 2013), it is expected that there are risks to the population of being at low population size, such as the loss of genetic variation and inbreeding depression. The scenarios do not fully explore the uncertainties in how small a population may get before it cannot be recovered (i.e. the models do not include depensatory processes). However, the sensitivity analysis with respect to the quasi-extinction threshold shows that the risk of extinction increases as this threshold is increased. Irrespective of the absolute value of this threshold, further reductions in abundance do take Outer Bay of Fundy salmon populations closer to this limit. As discussed above, there are risks associated with being at low population size that are expected to lead to lower fitness and thus a reduced capacity for population increase. Recovery is therefore expected to become more difficult if abundance continues to decline, as is expected for these populations with the continued passage of time.

6.0 ACKNOWLEDGMENTS

The authors thank the many people without whose hard work collecting the data these analyses would not have been possible; and Gerald Chaput for helpful comments on an earlier draft of this manuscript.

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8.0 TABLES

Table 2.1. Maximum likelihood estimates (M.L.E.) and their standard deviations (std. dev.) for the life history parameters characterizing freshwater productivity for the Atlantic Salmon populations in the Nashwaak River (using data from 1970 to 2011) and in the Tobique River (using data from 1989 to 2005). Also shown are the estimates of the maximum survival from egg to smolt and the asymptotic recruitment level derived for smolts. The conservation requirements are provided as indicators of the potential relative size of the populations. Estimates for the Tobique River population are from Gibson et al. (2009).

	Nashwaa	ak River	Tobique	e River
Parameter	M.L.E.	std. dev.	M.L.E.	std. dev.
Conservation Requirement:	12.80 mill	ion eggs	19.50 mill	ion eggs
Age and Stage specific parameter	er values:			
M _{Egg:}	0.96	0.01	0.96	0.02
α	0.54	0.07	0.93	0.28
R _{asy}	28.01	8.79	9.31	2.39
M _{Parr}	0.53	0.10	0.75	0.56
j ₂	0.61	0.06	0.37	0.07
j ₃	0.99	0.01	0.97	0.03
Egg to smolt dynamics:				
ă	0.007	0.001	0.005	n/a
\breve{R}_{asy}	104,430	36,178	27,009	n/a

Table 2.2. A summary of the average return rates (percent) of one sea-winter and two sea-winter wild Atlantic Salmon for the 1973 to 1982 (Past) and 2000 to 2009 (Present) time periods in the Nashwaak River. The values are the maximum likelihood estimates from the life history models. Two sets of values are provided: return rates to the river mouth and return rates through to spawning, including the recreational fishery removals. The difference between the two sets of values is an indicator of the effect of the recreational fishery on the proportion of the population surviving to spawn in each time period.

	Time I	Period
Parameter	1973-1982	2000-2009
Return rates to river mouth (%):		
1SW mean	6.18	4.95
1SW minimum	3.02	1.38
1SW maximum	12.14	11.48
2SW mean	4.04	1.10
2SW minimum	1.30	0.41
2SW maximum	9.07	1.96
Return rates to spawning - includi	ng recreational fishe	ery removals (%):
1SW mean	3.87	4.95
1SW minimum	1.97	1.38
1SW maximum	7.50	11.48
2SW mean	2.62	1.10
2SW minimum	0.82	0.41
2SW maximum	5.64	1.96

Table 2.3. A summary of the number of eggs produced per smolt throughout its life (EPS) for wild Atlantic for the 1973 to 1982 (Past) and 2000 to 2009 (Present) time periods in the Nashwaak River. The values are the maximum likelihood estimates from the life history models. Two sets of values are provided: EPS derived using return rates to the river mouth, and using survival through to spawning during the fall. The difference in the values is an indicator of the effect of the recreational fishery on the lifetime egg production per smolt in each time period.

	Time Period				
Parameter	1973-1982	2000-2009			
EPS using return rates to river mouth:					
mean	333	151			
minimum	117	49			
maximum	732	312			
EPS using survival through to spawning - ir	cluding recreational fishery rem	ovals:			
mean	215	151			
minimum	75	49			
maximum	454	312			

Table 2.4. A summary of the equilibrium population sizes and maximum lifetime reproductive rates for wild Atlantic Salmon in the Nashwaak River for the 1973 to 1982 and 2000 to 2009 time periods. The values are the maximum likelihood estimates from the life history model. Two sets of values are provided: those derived using return rates to the river mouth and those derived based on survival through to spawning escapement. The difference is an indicator of the effect of the recreational fishery (Nashwaak only) on the population dynamics in each time period.

	Time Period				
Parameter	1973-1982	2000-2009			
Values based on returns to mouth:					
Equilibrium egg deposition					
mean	20,805,000	1,761,400			
minimum	0	0			
maximum	62,444,000	18,550,000			
Equilibrium smolt abundance:					
mean	62,433	11,674			
minimum	0	0			
maximum	85,312	59,523			
Max. lifetime reproductive rate:					
mean	2.49	1.13			
minimum	0.88	0.37			
maximum	5.46	2.33			
Values based on survival to spawning escapement	t (includes the effect of the re	ecreational fishery:			
Equilibrium egg deposition:					
mean	8,408,700	1,761,400			
minimum	0	0			
maximum	33,463,000	18,550,000			
Equilibrium smolt abundance:					
mean	39,195	11,674			
minimum	0	0			
maximum	73,635	59,523			
Max. lifetime reproductive rate:					
mean	1.60	1.13			
minimum	0.56	0.37			
maximum	3.39	2.33			

Table 2.5. Equilibrium population sizes of Atlantic Salmon in the Tobique River, New Brunswick, for combinations of two smolt passage survival scenarios, two freshwater production scenarios and three levels of at-sea survival. Equilibrium population sizes above one half the conservation requirement are marked with an asterisks; those above the conservation requirement are denoted with two asterisks (adapted from Gibson et al. 2009).

		At-sea survival ^c							
		Ave	rage	Maxir	mum	Hypot	hetical		
Passage	Freshwater	Eggs	Smolt	Eggs	Smolt	Eggs	Smolt		
survival ^a	production ^b	(x10 ⁶)	(x10 ³)	(x10 ⁶)	$(x10^{3})$	(x10 ⁶)	(x10 ³)		
current	current	0.00	0.00	0.00	0.00	0.00	0.00		
current	improved	0.00	0.00	7.34	53.97	18.69*	86.14		
improved	current	0.00	0.00	0.85	3.40	4.84	12.21		
improved	improved	7.29	53.73	23.15**	93.06	43.90**	110.65		

Notes:

^asmolt passage survival: current = 0.547, improved = 1.00;

^bfreshwater production: current = parameter values in Table 5, improved = doubling survival of age 1+ parr and R_{asy} ; ^caverage at-sea survival = return rates of 3.2% and 0.9%, maximum = 6.4% and 1.6%, and hypothetical = 8% and 3%, for 1SW and 2SW salmon respectively.

Table 3.1. Probabilities of extinction and of recovery within 1 to 10 decades for the Nashwaak River Atlantic Salmon population. Two scenarios are shown, one based on the 1973-1982 dynamics (past dynamics) and one based on the 2000's dynamics (present dynamics). The same random numbers are used for each scenario to ensure they are comparable. Probabilities are calculated as the proportion of 2000 Monte Carlo simulations of population trajectories that either went extinct or are above the recovery target in the given year.

	Probability of	of Extinction	Probability of	of Recovery
Year	Present	Past	Present	Past
10	0.00	0.00	0.00	0.05
20	0.00	0.00	0.00	0.29
30	0.00	0.00	0.00	0.42
40	0.00	0.00	0.00	0.50
50	0.01	0.00	0.00	0.52
60	0.03	0.00	0.00	0.54
70	0.06	0.00	0.00	0.56
80	0.11	0.00	0.00	0.54
90	0.19	0.00	0.00	0.54
100	0.28	0.00	0.00	0.55

Table 4.1. At-sea survival rates used in the recovery scenario analyses for the Nashwaak River 1973-1982 dynamics (past) and one based on the 2000's dynamics (present). The intermediate fraction is the proportionate increase in at-sea survival between the past and present scenarios.

		Time	Period	
		Intermediate	Intermediate	
Life History Parameter	Present	1/3	2/3	Past
1SW return rate (%)	4.95	5.29	5.62	5.95
2SW return rate (%)	1.29	2.31	3.33	4.35
Fecundity (small)	3,430	3,357	3,285	3,212
Fecundity (large)	7,387	7,305	7,224	7,142
Proportion female (small)	0.408	0.349	0.290	0.231
Proportion female (large)	0.796	0.817	0.838	0.858

Table 4.2. Proportions of 2000 simulated population trajectories that either go extinct or meet the recovery target within 10, 20, 30 and 50 year time horizons based on recovery scenarios for the Nashwaak River Atlantic Salmon population. The marine scenarios reflect changes from the present levels (2000's) of at-sea survival to those in the past (1973-1982). The freshwater scenarios reflect increases in freshwater productivity from the present level (1) to 2 times the present level. The lettering for the runs corresponds to those in Figures 4.1 – 4.3. Extreme event scenarios are the average frequency of extreme events and the reduction in egg to fry survival corresponding to the event.

	Maria a	E		Droportion Extinct			Proportion Recovered				
	Marine	Freshwater	Extreme Event		Proportio			P		ecovered	
Run	Scenario	Scenario	Scenario	10 yr	20 yr	30 yr	50 yr	10 yr	20 yr	30 yr	50 yr
а	present	1	10 yr; 0.2	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00
b	present	1.2	10 yr; 0.2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
С	present	1.5	10 yr; 0.2	0.00	0.00	0.00	0.00	0.00	0.01	0.01	0.01
d	present	2	10 yr; 0.2	0.00	0.00	0.00	0.00	0.03	0.18	0.25	0.32
е	present	1.5	20 yr; 0.1	0.00	0.00	0.00	0.00	0.00	0.01	0.01	0.01
f	present	1.5	none	0.00	0.00	0.00	0.00	0.00	0.01	0.02	0.03
g	intermediate 1/3	1	10 yr; 0.2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
h	intermediate 1/3	1.2	10 yr; 0.2	0.00	0.00	0.00	0.00	0.00	0.02	0.04	0.06
i	intermediate 1/3	1.5	10 yr; 0.2	0.00	0.00	0.00	0.00	0.05	0.25	0.34	0.44
j	intermediate 1/3	2	10 yr; 0.2	0.00	0.00	0.00	0.00	0.33	0.84	0.89	0.92
k	intermediate 1/3	1.5	20 yr; 0.1	0.00	0.00	0.00	0.00	0.05	0.30	0.42	0.52
Ι	intermediate 1/3	1.5	none	0.00	0.00	0.00	0.00	0.05	0.38	0.54	0.63
m	intermediate 2/3	1	10 yr; 0.2	0.00	0.00	0.00	0.00	0.01	0.06	0.08	0.14
n	intermediate 2/3	1.2	10 yr; 0.2	0.00	0.00	0.00	0.00	0.05	0.28	0.39	0.49
0	intermediate 2/3	1.5	10 yr; 0.2	0.00	0.00	0.00	0.00	0.25	0.75	0.84	0.88
р	intermediate 2/3	2	10 yr; 0.2	0.00	0.00	0.00	0.00	0.71	0.98	0.99	1.00
q	intermediate 2/3	1.5	20 yr; 0.1	0.00	0.00	0.00	0.00	0.27	0.80	0.88	0.91
r	intermediate 2/3	1.5	none	0.00	0.00	0.00	0.00	0.30	0.89	0.94	0.96
S	past	1	10 yr; 0.2	0.00	0.00	0.00	0.00	0.05	0.29	0.42	0.52
t	past	1.2	10 yr; 0.2	0.00	0.00	0.00	0.00	0.20	0.68	0.78	0.83
u	past	1.5	10 yr; 0.2	0.00	0.00	0.00	0.00	0.52	0.94	0.96	0.97
v	past	2	10 yr; 0.2	0.00	0.00	0.00	0.00	0.89	1.00	1.00	1.00
w	past	1.5	20 yr; 0.1	0.00	0.00	0.00	0.00	0.56	0.95	0.97	0.98
х	past	1.5	none	0.00	0.00	0.00	0.00	0.61	0.99	1.00	1.00

Table 4.3. Proportions of 2000 simulated population trajectories that either go extinct or meet the recovery target within 10, 20, 30 and 50 year time horizons based on harm scenarios for the Nashwaak River Atlantic Salmon population. The marine scenarios reflect changes from the present levels (2000's) of at-sea survival, by decreasing this 10%, 30%, and 50%. The freshwater scenarios reflect decreases in freshwater productivity from the present level by 10%, 20%, 30% and 50%. The lettering for the runs corresponds to those in Figure 4.4. Extreme events are set to occur once every 10 years with a bad year scalar of 0.2.

		Freshwater		Proportic	on Extinct			Proportion	Recovered	
Run	Marine Harm	Harm	10 yr	20 yr	30 yr	50 yr	10 yr	20 yr	30 yr	50 yr
а	present	Present	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00
b	present	10%	0.00	0.00	0.00	0.07	0.00	0.00	0.00	0.00
С	present	20%	0.00	0.00	0.02	0.38	0.00	0.00	0.00	0.00
d	present	30%	0.00	0.00	0.11	0.85	0.00	0.00	0.00	0.00
е	present	50%	0.00	0.20	0.88	1.00	0.00	0.00	0.00	0.00
f	10%	Present	0.00	0.00	0.00	0.07	0.00	0.00	0.00	0.00
g	10%	10%	0.00	0.00	0.02	0.34	0.00	0.00	0.00	0.00
h	10%	20%	0.00	0.00	0.08	0.78	0.00	0.00	0.00	0.00
i	10%	30%	0.00	0.02	0.31	0.98	0.00	0.00	0.00	0.00
j	10%	50%	0.00	0.41	0.98	1.00	0.00	0.00	0.00	0.00
k	30%	Present	0.00	0.00	0.11	0.85	0.00	0.00	0.00	0.00
I	30%	10%	0.00	0.02	0.31	0.98	0.00	0.00	0.00	0.00
m	30%	20%	0.00	0.07	0.64	1.00	0.00	0.00	0.00	0.00
n	30%	30%	0.00	0.24	0.91	1.00	0.00	0.00	0.00	0.00
0	30%	50%	0.01	0.90	1.00	1.00	0.00	0.00	0.00	0.00
р	50%	present	0.00	0.03	0.45	1.00	0.00	0.00	0.00	0.00
q	50%	10%	0.00	0.10	0.74	1.00	0.00	0.00	0.00	0.00
r	50%	20%	0.00	0.28	0.93	1.00	0.00	0.00	0.00	0.00
S	50%	30%	0.00	0.57	0.99	1.00	0.00	0.00	0.00	0.00
t	50%	50%	0.02	0.98	1.00	1.00	0.00	0.00	0.00	0.00



Figure 1. Map showing the location of the Outer Bay of Fundy relative to the three other designatable units for Atlantic Salmon in the Maritimes.



Figure 2.1. Observed (points) and fitted (lines) of egg depositions and smolt counts for the Atlantic Salmon populations in the Nashwaak River as estimated with the life history model. The broken lines show 95% confidence intervals based on normal approximations.



Figure 2.2. Observed (points) and estimated (lines) return rates for one sea-winter and two sea-winter wild Atlantic Salmon for the Nashwaak population, as estimated with the life history model. The broken lines show 95% confidence intervals based on normal approximations.


Figure 2.3. Bayesian posterior probability densities for the average return rates of one sea-winter (left column) and two sea-winter (right column) during the 1973 to 1982 (top row) and 2000 to 2009 (bottom row) time periods for the Nashwaak River wild Atlantic Salmon population. The return rates are as estimated to the mouth of the river. The time periods refer to the years of smolt production.



Figure 2.4. Conceptual diagram showing how an equilibrium model can be used to analyze the dynamics of a fish population and to determine how a population will respond to either changes in life history parameter values or recovery actions. A Beverton-Holt model (a) is used to model the density-dependent relationship for survival from eggs to smolt. The slope at the origin of this model, which is the maximum number of smolts produced per egg in the absence of density dependent effects, changes as habitat quality changes, whereas changes in the amount of habitat changes the carrying capacity. The number of eggs produced per smolt throughout its life (b) changes with smolt-to-adult survival, fecundity, age-at-maturity or the number of time a fish spawns throughout its life. The population equilibrium (c) occurs at the population size where the production of smolts by eggs is equal to the production of eggs by smolts throughout their lives, and is the size at which the population will stabilize if all life history rates and the habitat carrying capacity remain unchanged. The population equilibrium changes as the values of the life history parameters change (from Gibson and Amiro 2007).



Figure 2.5. Bayesian posterior probability densities for the average numbers of eggs produced by a smolt throughout its life during the 1973 to 1982 (top row) and 2000 to 2009 (bottom row) time periods for the Nashwaak River wild Atlantic Salmon population. The vertical dashed lines show the maximum likelihood estimates from the model. The return rates are as estimated to the mouth of the river. The time periods refer to the years of smolt production.



Figure 2.6. Equilibrium analysis of the dynamics of the Atlantic Salmon population in the Nashwaak River. The points are the observed egg depositions and smolt production for the 1973 to 1982 (top panel) and the 2000 to 2009 (lower panel) egg deposition years. The curved, solid line represents freshwater production. The straight, dashed lines represent marine production as calculated at the minimum observed return rates, the mean observed return rates, and the maximum observed return rates for 1SW and 2SW adults during the two time periods. Dark shading indicates egg depositions above the conservation egg requirement, medium shading is between 50% and 100% the egg requirement, and the light shading is below 50% of the requirement.



Max. Lifetime Reproductive Rate

Figure 2.7. Bayesian posterior probability densities for the maximum lifetime reproductive rate during the 1973 to 1982 (top row) and 2000 to 2009 (bottom row) time periods for the Nashwaak River wild Atlantic Salmon population. The vertical dashed lines show the maximum likelihood estimates from the model. The return rates are as estimated to the mouth of the river. The time periods refer to the years of smolt production.



Figure 2.8. Equilibrium analysis of the Tobique River salmon population dynamics given current fish passage mortality of 45.3% (top panel) and a scenario if fish passage mortality was reduced to zero (lower panel). In both panels, the curved, solid line is the current estimated freshwater production and current marine production is shown by the solid straight line. The curved dashed line is the hypothetical scenario where the carrying capacity for age 1 parr is doubled to 18.6 parr/100 m² and survival of parr age 1 and older is doubled to 0.49 per year. The middle dashed line is the marine production calculated using the maximum observed rates on the Nashwaak, and the dashed line on the right represents a hypothetical scenario of 8% and 3% return rates for 1SW and 2SW salmon respectively. Dark shading indicates egg depositions above the conservation egg requirement, medium shading is between 50% and 100% the egg requirement, and the light shading is below 50% of the requirement (from Gibson et al. 2009).



Figure 3.1. Simulated median abundance (solid line) with the 10th and 90th percentiles (dashed lines) for each of five life stages from Monte Carlo simulations of the Nashwaak River Atlantic Salmon population viability model. Two scenarios are shown, one based on the 1973-1982 dynamics (right panels) and one based on the 2000's dynamics (left panels). The graphs summarize 2000 simulations for each scenario.



Figure 3.2. The probability of extinction and the probability of recovery as a function of time for the Nashwaak River Atlantic Salmon population. Two scenarios are shown, one based on the 1973-1982 dynamics (right panels) and one based on the 2000's dynamics (left panels). Probabilities are calculated as the proportion of 2000 Monte Carlo simulations of population trajectories that either when extinct or met the recovery target.



Figure 3.3. Sensitivity analysis of the effects of extreme events on the viability of Nashwaak River Atlantic Salmon. The graphs summarize 2000 simulations for each scenario. The median abundance (solid line), and the 10th and 90th percentiles (dashed lines) are shown. Panels on the right and left are based on the 1973-1982 dynamics and 2000's dynamics respectively. The top row shows a deterministic run without extreme events, the second row a stochastic run without extreme events, the third row a stochastic run without extreme events (the base model), the fourth row the effect of decreasing the frequency and increasing the magnitude of extreme events, and the bottom row the effect of increasing the frequency of extreme events.

Nashwaak River



Figure 3.4. The effect of further reductions in population size on the abundance trajectories using base model for the Nashwaak River Atlantic Salmon population. The graphs summarize 2000 simulations for each scenario. The median abundance (solid line), and the 10th and 90th percentiles (dashed lines) are shown. Panels on the right and left are based on the 1973-1982 dynamics and 2000's dynamics respectively. The top row shows the trajectories using the 2008-2012 average abundance estimate (896 small salmon and 263 large salmon) as the starting population size. The other rows show the effects of starting at 50%, 25% and 10% of the starting abundance respectively.



Figure 3.5. The probability of extinction (top row) and the probability of recovery (bottom row) as a function of time for the Nashwaak River Atlantic Salmon population showing the effects of further reductions in population size. Scenarios are based on the 1973-1982 dynamics (right panels) and on the 2000's dynamics (left panels). The thick solid lines show the probabilities when the starting population size is the 2008-2012 average abundance estimate (896 small salmon and 263 large salmon). The other lines show the effects of starting at 50%, 25% and 10% of this abundance (moving away from the solid line, respectively). The 2012 abundance estimates (29 small salmon and 63 large salmon) produce the thin solid line.



Figure 3.6. Sensitivity analyses showing the effect of the quasi-extinction threshold on the probability of extinction (top row) and the probability of recovery (bottom row) for the Nashwaak River Atlantic Salmon population. Scenarios are based on the 1973-1982 dynamics (right panels) and on the 2000's dynamics (left panels). The solid lines show the probabilities when the quasi-extinction threshold is set at 15 females. The dashed lines show the effects of setting the threshold at 30, 50 and 100 females (moving away from the solid line, respectively).



Figure 4.1. The effects of increasing at-sea survival and freshwater productivity on the simulated abundance of eggs for the Nashwaak Atlantic Salmon population. The graphs summarize 2000 simulations for each scenario. The median abundance (solid line), and the 10th and 90th percentiles (dashed lines) are shown. Panels on the right and the left are based on the 1973-1982 (past) and 2000's (present) at-sea survival respectively, and the two middle panels show scenarios using survivals increased by 1/3 and 2/3's of the difference in these values. The return rates of 1SW and 2SW salmon and survival between repeat spawning events are increased. The 2000's freshwater production is used in all scenarios. The top four rows show the effect of increasing freshwater productivity by factors of 1 (no change), 1.2 (20% increase), 1.5 (50% increase) and 2.0 (100% increase). The bottom two rows show the effect of changing the frequency of event events to an average of 1 every 20 years (5th row) and to no extreme events (bottom row).



Figure 4.2. The effects of increasing at-sea survival and freshwater productivity on the probability of extinction for the Nashwaak River Atlantic Salmon population. Panels are described in the caption for Figure 4.1.



Figure 4.3. The effects of increasing at-sea survival and freshwater productivity on the probability of meeting the recovery target for the Nashwaak River Atlantic Salmon population. Panels are described in the caption for Figure 4.1.



Figure 4.4. The effects of decreasing at-sea survival and freshwater productivity on the extinction probability for the Nashwaak Atlantic Salmon population. The graphs summarize 2000 simulations for each scenario. The median abundance (solid line), and the 10th and 90th percentiles (dashed lines) are shown. Panels on the left are based on the 2000's (present) at-sea survival, and the panels moving to the right show the effects of decreasing survival by 10%, 30% and 50% from the present values. The rows show the effect of decreasing freshwater productivity by factors of 1 (0% decrease), 0.9 (10% decrease), 0.8 (20% decrease), 0.7 (30% decrease) and 0.5 (50% decrease).

10.0 APPENDICES

APPENDIX 1. THE STATISTICAL, LIFE-HISTORY BASED POPULATION DYNAMICS MODEL USED FOR ESTIMATING LIFE HISTORY PARAMETER VALUES AND ANALYSING THE DYNAMICS OF THE NASHWAAK RIVER ATLANTIC SALMON POPULATION

This model is very similar to that developed by Gibson and Bowlby (2013) for analyzing the dynamics of the LaHave River and St. Mary's River Atlantic Salmon populations. Here, the model is modified to reflect differences in the available information about survival between spawning events for the Nashwaak River population and for the LaHave River population. The text in this Appendix is taken almost verbatim from Gibson and Bowlby (2013).

The life history parameter estimates provided in Section 2.2, as well as the information on population dynamics in Section 2.5, were derived using a statistical, life-history-based population dynamics model developed by Gibson et al. (2008b; 2009). The method follows the general theory developed by Fournier and Archibald (1982) and Deriso et al. (1985) for statistical catch-at-age models for stock assessment that allows auxiliary data to be incorporated for model fitting. The approach used here is similar in that multiple indices (auxiliary data) are used to derive estimates of the age- and stage-specific abundances and survival rates required to analyze the dynamics of these populations. The life history parameter estimates are then used to determine how recovery actions may be expected to change population size and viability.

As described in Section 2, the population dynamics model consists of two parts: a freshwater production model that provides estimates of the expected smolt production as a function of egg deposition, and a lifetime egg-per-smolt model that provides estimates of the rate at which smolts produce eggs throughout their lives. These components are combined via an equilibrium analysis that provides estimates of the abundance at which the population would stabilize if the input parameters remained unchanged. This combined model is then used to evaluate how equilibrium population size has changed through time, as well as how the population would be expected to change in response to changes in carrying capacity, survival, or life stage transition probabilities, as described in Section 2.5.

The structure of the population dynamics model (freshwater production model component and the lifetime egg-per-smolt model component) is described in Sections A1.1 and A1.2. The equilibrium model is described in Section A1.3. The statistical procedures used for parameter estimation and model fitting are described in Section A1.4.

A1.1 Freshwater Component of Life Cycle (Eggs to Smolts)

Model indices and parameter definitions for the freshwater component of the model are provided in Table A1.1 and the equations for characterizing dynamics in fresh water are provided in Table A1.2. A description of this model follows below.

The number of age-0 juveniles (or fry), at the time of the electrofishing surveys in the summer, is a function of egg deposition in the previous fall (calculated from total adult escapement in each year) multiplied by the egg to age-0 survival rate (Equation 1, Table A1.2).

Density dependence was incorporated into the model via survival from age-0 to age-1 using a Beverton-Holt function, based on the results of Gibson (2006). Abundance of age-1 juveniles is a function of the maximum survival rate between age-0 and age-1, α , the asymptotic density of age-1 parr (maximum number per 100 m² habitat units, R_{asy}), an electrofishing catchability coefficient or scalar, *h*, and the probability that a fish emigrates as a smolt at age-1, j_1 (Equation 2, Table A1.2). The product, $R_{asy}h$ is the carrying capacity of the river for age-1 parr.

The model is formulated this way because the electrofishing data, used to estimate the number of parr, is reported as a density (number per 100 m^2), whereas the interest here is in the total number of parr in the river. The parameter *h*, which can be estimated within the model, is used to scale the parr density to the total abundance. Estimating the parameter, rather than using the measured number of habitat units, corrects for potential issues that would arise if the electrofishing sites fished each year were not representative of the entire river (Gibson et al. 2009).

An implicit assumption made here is that the density of all age classes of parr can be scaled up to their respective abundances using a single value of h. This assumption is made because a set of age-specific catchabilities and mortalities would be identifiable (covariance of 1) in the model without some sort of auxiliary information about one parameter or the other (*sensu* Quinn and Deriso 1999). If the electrofishing sites are selected such that one age class is over- or under-represented in the sampling, the resulting age-specific mortality estimates would be biased, although the overall freshwater production curve would likely remain representative because the annual egg depositions and smolt abundance estimates do not have the same catchability issues.

The number of age-2 and older parr is determined by the number of parr in the cohort in the previous year (P_{t-1} ,_{*a*-1}), density-independent survival of parr (M_{Parr}), and the age-specific probability of smoltification, j_a (Equation 3, Table A1.2). The number of smolt in each age and year class, $S_{t,a}$, is determined similarly (Equation 4, Table A1.2). The maximum age at smoltification was assumed to be four for the Nashwaak River population, based on the observed ages of smolts during smolt monitoring in these rivers.

By combining the life stage-specific parameter estimates into a two parameter Beverton-Holt spawner recruitment function, it is possible to describe smolt production as a function of egg deposition. This is particularly convenient for the equilibrium population size calculations below to calculate overall freshwater productivity. Both parameters, the slope of the function at the origin (the maximum number of smolts produced per egg in the absence of density dependence) and the asymptotic recruitment level for smolts (the number of smolts that would be produced in a cohort if the egg deposition was infinite), can be calculated directly from the estimated parameters (Equations 5 and 6, Table A.1.2).

A1.2 Lifetime Egg-per-smolt Model

The freshwater component of the life history model is used to characterize survival, productivity and stage-transition probabilities from the egg to the smolt stage, whereas the second part of the life history model characterizes the manner in which smolts produce eggs throughout their lives, abbreviated as EPS (for eggs-per smolt). Model indices and parameter definitions for the EPS component of the model are provided in Table A1.3 and the equations characterizing these dynamics are provided in Table A1.4.

An important demographic parameter for evaluating the potential for population recovery is the rate at which smolts return to spawn for the first time, either as 1SW or 2SW salmon. One of the limitations of Atlantic Salmon data is that the smolt abundance time series available for calculating return rates of adults are relatively short (1998- present for the Nashwaak River population) and the data are only available in recent years when abundance is low and decreasing. This makes it impossible to directly calculate return rates (indicative of marine survival) in earlier years, when abundance was higher, and to determine how population dynamics have changed such that populations are no longer viable. To address this issue, the estimated smolt abundance from the freshwater production model (described above) was used to extend the time series available for calculating return rates. One of the data inputs for the

Nashwaak River population is the estimated annual spawning escapement of large and small salmon in the Nashwaak River. Estimates of the survival from the smolt life stage through to spawning escapement for 1SW and 2SW salmon are calculated (Equation 1, Table A.1.4) by dividing the number of salmon in each sea-age class by the estimated number of smolts emigrating either one or two years earlier (using smolt abundance estimates from the freshwater production model).

The sum of the mortalities associated with the recreational fishery (as a result of either retention or hook-and-release mortality) and the escapement for each sea-age group of adults provides an estimate of the returns of 1SW and 2SW fish to the river in a given year. Exploitation rates in fresh water are calculated from these values (Equation 2, Table A.1.4). Return rates to the mouth of the river for each sea-age group are calculated from the group-specific exploitation rates and escapement estimates, as well as the estimated number of smolts emigrating either one year or two years earlier (Equation 3, Table A.1.4).

The EPS is the sum of the lifetime egg production of 1SW and 2SW salmon multiplied by their respective return rates (Equation 4, Table A.1.4). The lifetime egg production for each sea-age category is a function of their size-specific fecundity, annual survival between spawning events, maximum number of spawnings, their sea-age specific (1SW or 2SW) return rates as either alternate-year or consecutive-year repeat spawners (Equations 4.1 and 4.2, Table A.1.4) and their subsequent probabilities of returning to spawn a third time.

A1.3 Equilibrium Calculations

As discussed in Section 2.5, equilibrium models are a useful way of evaluating the effects of human activities and life history changes on fish populations. The equilibrium egg deposition and number of smolts are denoted with asterisks to differentiate them from parameters in the freshwater life history model. Similarly, $\tilde{\alpha}$ and \tilde{R}_{asy} represent the maximum rate of population growth and equilibrium population size for smolts in freshwater, respectively. The egg and smolt equilibrium values are calculated as follows:

Equilibrium egg deposition ($Eggs^*$) is:

$$Eggs^* = \frac{(\breve{\alpha} EPS - 1)\breve{R}_{asy}}{\breve{\alpha}},$$

and the equilibrium number of smolts (S^*) is found by substituting $Eggs^*$ into the freshwater production model:

$$S^* = \frac{\breve{\alpha}Eggs^*}{1 + \frac{\breve{\alpha}Eggs^*}{\breve{R}_{asy}}}.$$

For the full derivation, see Gibson et al. (2009).

A1.4 Parameter Estimation and Statistical Considerations

Maximum Likelihood

Parameter estimates for the freshwater production model were obtained by simultaneously fitting the model to the observed data using maximum likelihood by minimizing the value of an objective function, *OFV*, (Quinn and Deriso 1999). The *OFV* equals the sum of the negative log likelihoods for the juvenile electrofishing data ($\ell_{electro}$), the smolt age-frequency data (ℓ_{age}), the egg deposition data (ℓ_{egg}) and the smolt count data (ℓ_{smolt}). Lognormal error structures (Myers

et al. 1995) were used for all likelihoods except the smolt age-frequency data, for which a multinomial likelihood (Quinn and Deriso 1999) was used. The objective function and the likelihood equations are provided in Table A1.5.

Estimating the variance for multiple lognormal likelihoods is problematic without other information about their variability. Gibson and Amiro (2003) had similar issues estimating the mean standard deviation of the likelihood estimates (σ) for all components of a similar model. Following their approach, the average values obtained by Myers et al. (1995) from spawner-recruit relationships of 15 populations of Atlantic Salmon were used in this analysis. For recruitment ages of 0, 1 and 2, σ equaled or averaged 0.33 (n = 1), 0.33 (n = 4) and 0.58 (n = 1), respectively, where n is the number of populations considered. Based on these results, σ was set equal to the median value, 0.33, for all age categories.

The parameters for the freshwater production model are listed in Table A1.1. The specific demographic parameters estimated are egg and parr mortality (M_{Egg} and M_{Parr}), the maximum

rate of population increase for age 1 parr (α), the carrying capacity for age 1 parr (R_{asy}), and

the smoltification probabilities at age (j_a). In addition, annual egg depositions for each year,

and the electrofishing scalar were estimated in the model. Attempts were made to estimate parameter values for two time periods (by splitting the model and data into an earlier and later time periods), but these were not successful, likely due to a lack of contrast in the data for the two time periods.

The freshwater production model was programmed using AD Model Builder (ADMB) (Fournier 1996), which uses the C++ auto-differentiation library for rapid fitting of complex non-linear models, has Bayesian and profile likelihood capabilities, and is designed specifically for fitting these and similar types of models. The change in the Akaike Information Criterion (AIC) was used to help assess the trade-off between model fit to the data and the number of parameters in the candidate model (Hilborn and Mangel 1997). The model with the lowest AIC was generally selected as the preferred model. A similar approach was used to help select the best data input (for example, to choose whether to use standardized or un-standardized electrofishing data). The model was run using several different sets of starting values to ensure that the model was not converging at a local (rather than a global) minimum. Standard errors for parameter estimates were calculated from the variance and correlation matrix generated by the Delta method (Efron and Tibshirani 1993). This is standard output from ADMB.

Bayesian Analyses

Bayesian methods provide a powerful tool for assessing uncertainty in fisheries models (McAllister et al. 1994). Punt and Hilborn (1997) and McAllister and Kirkwood (1998) have reviewed their fisheries applications. The posterior probability distributions resulting from Bayesian analyses show the uncertainty in model or policy parameters including both estimation uncertainty, as well as prior information about their values (Walters and Ludwig 1993). ADMB uses a Markov Chain Monte Carlo (MCMC) algorithm (Carlin and Louis 1996) to approximate the posterior distribution for parameters of interest. MCMC is a stochastic simulation method used to evaluate complex integrals in order to derive posterior distributions. ADMB uses the Metropolis Hastings algorithm (Chib and Greenberg 1995) to generate the Markov chain, using a multivariate normal distribution based on the variance-covariance matrix for the model parameters as the proposal function. If the chain is long enough, the posteriors will be reasonably well approximated.

Uniform bounded priors were assumed for all model parameters. Bounds were wide enough so as not to influence the fit. The posterior distribution was derived by sampling every 4,000th iteration from a chain consisting of 4,000,000 iterations of the MCMC algorithm after a burn in of

400,000 iterations. This level of thinning was sufficient to ensure that autocorrelation in the chain was not problematic. Convergence of the Markov chain was inferred informally by comparing the similarity of the 10th and 90th percentiles of the posterior densities based on the first 2,000,000 iterations with those based on the second 2,000,000 iterations, and by comparison of the posterior densities from several chains (Gamerman 2000).

Table A1.1. Parameters and indices used in the freshwater production model. Indices are used as subscripts for years and age classes; estimated parameters are those that are estimated by the model using maximum likelihood; and derived parameters are those values calculated from the estimated parameters. From Gibson and Bowlby (2013).

Model Parameter	Description	Туре
t	Time in years	index
а	Juvenile age	index
Egg_t	Egg deposition in year <i>t</i>	estimated
$M_{_{Egg}}$	Egg-to-fry mortality rate	estimated
$P_{t,0}$	Abundance of fry (age-0) in year t	derived
$D_{t,0}$	Density of fry (age-0) in year t	derived
α	Maximum survival from age-0 to age-1 (slope at the origin of the Beverton-Holt model)	estimated
R _{asy}	Asymptotic age-1 density (N/100 m ²)	estimated
h	Electrofishing scalar (habitat area in m ²)	constant or estimated
$P_{t,a}$	Abundance of parr of age <i>a</i> in year <i>t</i>	derived
$D_{t,a}$	Density of parr of age <i>a</i> in year <i>t</i>	derived
M _{Parr}	Parr mortality rate (age-1 and older)	estimated
${j_a}$	Probability of smolting at age a	estimated
$S_{t,a}$	Abundance of smolt of age <i>a</i> in year <i>t</i>	derived
σ	Standard deviation for the likelihood functions	constant (0.33)
ă	Maximum number of smolts produced per egg (slope at the origin of the Beverton-Holt model)	derived
\breve{R}_{asy}	Carrying capacity for smolts	derived

Equation Number	Description	Equation
1	Abundance of fry (age-0) in year <i>t</i>	$P_{t,0} = Egg_{t-1}(1 - M_{Egg})$
2	Abundance of age-1 parr in year <i>t</i> (incorporating density dependence)	$P_{t,1} = \frac{\alpha P_{t-1,0}}{1 + \frac{\alpha P_{t-1,0}}{R_{asy}h}} (1 - j_1)$
3	Abundance of age-2 and older parr in year t	$P_{t,a} = P_{t-1,a-1}(1 - M_{Parr})(1 - j_a)$
4	Smolt abundance in year <i>t</i> of age <i>a</i>	$S_{t,a} = \left\{ P_{t-1,a-1}(1 - M_{Parr})(j_a) \qquad a = 1,2,3,4 \right\}$
5	Maximum survival from egg to smolt	$\breve{\alpha} = \alpha (1 - M_{Egg}) \left[j_1 + \sum_{a=2}^{4} \left[j_a \left(\prod_{k=1}^{k=a-1} (1 - j_k) \right) (1 - M_{Parr})^{a-1} \right] \right]$
6	Carrying capacity of the river for smolts	$\breve{R}_{asy} = R_{asy} h \left[j_1 + \sum_{a=2}^{4} \left[j_a \left(\prod_{k=1}^{k=a-1} (1 - j_k) \right) (1 - M_{Parr})^{a-1} \right] \right]$

Table A1.2. Model equations for the freshwater production component of the population dynamics model. From Gibson and Bowlby (2013).

Table A1.3. Parameters and indices used in the lifetime egg-per-smolt model. Indices are used as subscripts for years and age classes, derived parameters are those values calculated from the estimated parameters, and data are values such as counts that are used as model inputs for calculations (assumed known without error). Modified from Gibson and Bowlby (2013).

Model Parameter	Description	Туре
С	Number of years as an immature salmon at sea	index
r	repeat spawning strategy: <i>alt</i> - alternate year repeat spawner; <i>cons</i> - consecutive year repeat spawer	index
Esc _{t,c}	Spawning escapement of salmon of sea- age c in year t	data
$C_{t,c}$	Number of salmon of sea-age <i>c</i> removed by the recreational fishery in year <i>t</i>	data
U _{t,c}	Exploitation rate of salmon of sea-age c in year t	derived
$p_{c,r}$	Probability that a salmon of sea age <i>c</i> returns as a repeat spawner utilizing strategy <i>r</i>	data
$p_{c,r,r}$	Probability that a salmon of sea age <i>c</i> that has used strategy <i>r</i> utilizes strategy <i>r</i> when spawning for a third time	data
f_1	Fecundity of 1SW females (# of eggs)	data
f_2	Fecundity of MSW females (# of eggs)	data
RR_c^{river}	Return rates of salmon of sea-age <i>c</i> to the mouth of the river	derived
$RR_{c}^{escapement}$	Return rates of salmon of sea-age <i>c</i> to spawning escapement	derived
EPS	Lifetime egg production per smolt	derived

Equation		
Number	Description	Equation
1	Return rates to the assessment facility/location for salmon of sea-age c in smolt year class t	$RR_{t,c}^{escapement} = \frac{Esc_{t+c,c}}{\sum_{a=2}^{4} S_{t,a}}; c = 1, 2$
2	Exploitation rates for salmon of sea- age c in smolt year class t	$u_{t,c} = \frac{C_{t+c,c}}{C_{t+c,c} + Esc_{t+c,c}}; \ c = 1,2$
3	the mouth of the river for salmon of sea- age c in smolt year class t	$RR_{t,c}^{river} = \frac{Esc_{t+c,c} / (1 - u_{t,c})}{\sum_{a=2}^{4} S_{t,a}}; \ c = 1, 2$
4	Lifetime egg deposition per smolt in smolt year class <i>t</i>	$EPS_{t} = \sum_{c=1}^{2} RR_{t+c,c}^{escapement} Egg_{c}$, where:
4.1	Lifetime egg deposition for a 1SW salmon	$Egg_{1} = f_{1} + p_{1,alt} f_{2} (1 + p_{1,alt,alt} + p_{1,alt,cons}) + p_{1,cons}f_{2} (1 + p_{1,cons,alt} + p_{1,cons,cons})$
4.2	Lifetime egg deposition for a 2SW salmon	$Egg_{2} = f_{2}(1 + p_{2,alt} (1 + p_{2,alt,alt} + p_{2,alt,cons}) + p_{2,cons} (1 + p_{2,cons,alt} + p_{2,cons,cons}))$

Table A1.4. Model equations for the lifetime egg-per-smolt component of the population dynamics model.Parameter definitions are provided in Tables A1.3 and A1.1. MModified from Gibson and Bowlby (2013).

Equation Number	Description	Equation
1	Egg likelihood	$\ell_{egg} = -n \ln \sigma_{egg} \sqrt{2\pi} - \sum_{t} Egg_{t}^{obs} - \frac{1}{2\sigma_{egg}^{2}} \sum_{t} \left(\ln Egg_{t}^{obs} - \ln Egg_{t} \right)^{2}$
2	Electrofishing likelihood	$\ell_{electrofishing} = \sum_{a} \left(-n \ln \sigma_{elect} \sqrt{2\pi} - \sum_{t} D_{t,a}^{obs} - \frac{1}{2\sigma_{elect}^2} \sum_{t} \left(\ln D_{t,a}^{obs} - \ln(P_{t,a} / h) \right)^2 \right)$
3	Smolt likelihood	$\ell_{smolt} = -n \ln \sigma_{smolt} \sqrt{2\pi} - \sum_{t} S_{t}^{obs} - \frac{1}{2\sigma_{smolt}^{2}} \sum_{t} \left(\ln S_{t}^{obs} - \ln S_{t} \right)^{2}$
4	Smolt age-frequency likelihood	$\ell_{age}^{smolt} = \sum_{t} \log \left(\frac{n_{smolt,t}!}{(x_{smolt,t,1}!)(x_{smolt,t,2}!)(x_{smolt,t,r}!)} p_{smolt,t,1}^{x_{smolt,t,1}}p_{smolt,t,r}^{x_{smolt,t,r}} \right)$
5	O.F.V. value	$O.F.V. = -(\ell_{egg} + \ell_{smolt} + \ell_{electrofishing} + \ell_{age}^{smolt})$

Table A1.5. Likelihood functions and the objective function used for fitting the freshwater component of the population dynamics model. From Gibson and Bowlby (2013).

APPENDIX 2. LIFE HISTORY PARAMETER ESTIMATION FOR THE NASHWAAK RIVER ATLANTIC SALMON POPULATION

The life history parameter estimates for the Nashwaak River Atlantic Salmon population, provided in Section 2.2, as well as the information on the population's dynamics in Section 2.4, were derived using the statistical, life-history-based population dynamics model presented in Appendix 1. The application of the model to this population is described in this appendix. Included is a description of the data series used in the analyses, alternate model runs, interpretation of results, as well as the reasoning and biological justification for selecting the preferred model.

A2.1 Data

Recreational Fishery Statistics

Catch and effort data from the annual recreational Atlantic Salmon fishery (Table A2.1) have been collected using two methods: DFO collated statistics were used from 1970 until 1989 (Penny and Marshall 1984; Marshall 1987; O'Neil et al. 1987; 1989; 1991; 1996) and provincial catch data for small (1984-97) and large released (1990-94) have been adjusted using previous ratios when both datasets existed; for example, DFO/Prov stats. Effort data from 1970 to 1997 is tabled from provincial license database (O'Neil et al. 1996; K. Collet pers. comm.). Effort was estimated in rod days where any portion of a day fished by one angler was recorded as one rod day (effort is reported here but not used in the model). Nashwaak River has been closed to all recreational salmon fishing since 1998 (Jones et al. 2014).

The recreational fishery statistics are used in this analysis to estimate the smolt-to-adult return rates through to spawning escapement (i.e. after any removals by the recreational fishery). This was done by subtracting the number of virgin 1SW and 2SW salmon estimated to have been removed by the fishery from the numbers of adult returns, under the assumption that virtually all fishing occurs upstream of the counting fence. The numbers of virgin 1SW and 2SW wild salmon removed by the fishery are calculated from the number of large and small salmon reported in the recreational fishery statistics using the biological characteristics of the population sampled (Table A2.2). A hook-and-release mortality estimate of 4% was applied in the analysis, consistent with recent assessments (e.g. DFO 2011). Additionally the recreational fishery statistics were used to estimate abundance for those years in which the counting fence was not operated (and 1975), as described below.

Adult Abundance and Biological Characteristics

From 1993 until 2012, most adult salmon captured at a counting fence, operated by DFO and local First Nations, were counted, measured for fork length, categorized as either small or large salmon, externally sexed (male, female), classified as hatchery or wild, and marked with a hole punch. Further sampling details (including proportions and exceptions to general protocols), annual dates of operation, counts, return estimates, spawning escapement estimates and assessment method have been tabled in Jones et al. (2014). The counting fence was also operated for three years during the 1970's and annual assessments were completed in 1972-1973 but not in 1975 (Penny and Marshall 1984). Adult abundance and spawning escapement were estimated for small and large salmon from 1970 until 1993 (except 1972-1973) using recreational catch data. Catch rates (small: 0.48, 0.28 and large: 0.49, 0.27) derived by Penny and Marshall (1984) were averaged and then applied to recreational catch data to estimate annual small and large salmon abundance (Table A2.3). Biological characteristic data (mean length, proportion female, etc.) collected from salmon captured at the counting fence was applied to spawner escapement estimates to estimate annual egg depositions. In years when the fence not operated average biological characteristics information from other years was used; the mean values from 1970's were used for the 1970-1983 time period while the mean

values from 1993 to 2011 were applied to the 1984 to 1992 time period. This break year of 1984 was used because of management changes that occurred that year, including closure of commercial fishery and mandatory hook and release of all large salmon.

The adult counts and biological characteristics are used for three purposes. First, these data are used to estimate annual egg deposition (described below). Second, the data are used to determine the number of 1SW and 2SW first-time spawning salmon that return to the river to spawn. Lastly, these estimates are then used to calculate the smolt-to-adult return rates to the spawning escapement as described in Appendix 1.

The repeat spawning dynamics of salmon in the Nashwaak River population includes both alternate and consecutive spawners that represent less than 10% of the total returns in all years since the counting fence resumed operation in 1993. Mean survival of 1SW and 2SW salmon from 1st spawning to 2nd spawning were 3.1% and 9.0% (alternate and consecutive combined), respectively based on the maiden recruits from 1993 to 2009 (Table A2.4).

Egg Deposition Time Series

The annual egg depositions in the Nashwaak were calculated using the estimates of small (1SW) and large (MSW) salmon, their biological characteristics, and a length-fecundity relationship for female salmon destined for tributaries upriver of Mactaquac Dam (Marshall and Penny 1983). The fecundities of 1SW and MSW salmon have changed through time as a result of changes in the mean length and sex ratios in the two size classes (Tables A2.5, A2.6). The average fecundities from the 1970's was used to calculate the annual egg depositions for the years 1970 to 1983, and the average fecundities from 1993 to 2011 were used for the years 1984 to 1992. The annual fecundity estimates (Table A2.5) were used from 1993 to 2011. The egg deposition time series used in the model is provided in Table A2.3.

A key decision in calculating this series was whether the series should include both cultured and wild salmon, or whether only wild salmon should be used in its derivation. Although cultured salmon have been found to have lower spawning success relative to wild individuals (McGinnity et al. 2004; Weir et al. 2004; Jonsson and Jonsson 2006; Chilcote et al. 2011), they are still expected to contribute to subsequent juvenile production. At present, there is no way to identify whether juvenile salmon in this population are the progeny of cultured or wild salmon spawning in the wild. Therefore, the decision was made to include cultured salmon when calculating the number of eggs deposited each year (Table A2.3). The proportion of the MSW salmon component (which includes repeat-spawners) that are 2SW salmon, as well as the proportions of 1SW and MSW salmon that are of wild origin, based on sampling of the adult population. If no adult sampling occurred (no fence operation) then hatchery returns were estimated using smolt-to-adult return rates from Mactaquac.

Smolt Abundance and Biological Characteristics

The annual smolt migration for the Nashwaak salmon population was monitored from 1998 to 2012. A collaborative project between DFO, Nashwaak Watershed Association Inc. (NWAI) and Atlantic Salmon Federation to estimate the wild smolt production of the Nashwaak River has been ongoing since 1998. Oromocto First Nation has also participated since 2010. One or two American constructed rotary screw traps (RST) have been installed on an annual basis usually from mid-April until late-May in the main stem of the Nashwaak River just downriver of Durham Bridge (Chaput and Jones 2007). The RSTs were usually checked once daily from throughout the peak migration period and less frequently (every other day) at start of operation and as the daily catches decreased. All unmarked smolts were identified for origin (wild or hatchery). From 1998 until 2001 smolts (mostly wild origin) were captured, marked and released from a counting fence that was operated on the Tay River in order estimate the efficiency of the RST. Starting in

2001, a portion of the smolts were marked with either numbered streamer tags or caudal clip and released upriver in order to estimate the capture efficiencies of the RST(s).

Biological characteristics are collected from a sample of smolts captured during the assessment. The fork length and weight of sampled individuals is recorded and a scale sample is collected to determine the smolt's age. Abundance estimates and the number of sampled smolts in each age category are provided in Table A2.7 (the numbers in category are provided, rather than the proportions because this is how the data are input into the model). The time period over which smolt data has been collected is relatively short in comparison with the adult times series.

Abundance of Fry and Parr

The relative abundance of age-0 (fry), age-1 and age-2+ (collectively known as parr) juvenile salmon is determined by electrofishing. Note that here, the notation 2+ is used to denote a plus group consisting of all parr age 2 and older, consistent with the way this notation is used for other species (Quinn and Deriso 1999).

Four key decisions had to be made about the juvenile density data in the model: how to best estimate site-specific juvenile abundance from the data; how to best determine abundance-at-age; whether data from all sites should be included in the analysis; and whether the data should be standardized to correct for changes in the location of sites from year-to-year.

With the exception of 1980, densities of juvenile salmon have been monitored at least three of the ten index sites on the Nashwaak River on an annual basis since 1968. Densities prior to 1980 along with site characteristics and locations were reported by Francis (1980). Densities (number of fish per 100 m² of habitat) of age-0 and older parr at these sites were derived using three methods: removal method using multiple sweeps and barrier nets (Francis 1980), markrecapture techniques (Jones et al. 2004) using the adjusted Petersen method (Ricker 1975) or a mean probability of capture derived in Jones et al. (2004). In most years, the numbers of parr by age were determined from stratified sampling of large parr in 0.5 cm length intervals. Generally, one parr was scale sampled for each interval. If scale sampling was not completed in a particular year, then a length frequency distribution plot was used to partition the catches into age classes. When mark-recapture techniques were used, the number of age-0 parr or fry for the site was determined by applying the capture efficiency for age-1 and older parr to the number of fry captured during the marking pass. Also a mean probability of capture was applied if zero parr were marked or recaptured or if only the marking pass was completed (Jones et al. 2004). The densities from seven of the ten barrier sites have been adjusted to account for the expanded sites for when mark and recapture techniques were initiated in 1990 and 1991 (Marshall et al. 2000; updated in Jones et al. 2014). In addition to these 10 sites, the Nashwaak River juvenile surveys were expanded from 2004 to 2008, when an additional 10 or so sites were electrofished, but this data is not used in this analysis.

The densities presented are for wild (or adipose fin present) parr only. For the most part, prior to 1998 all fall fingerling and unfed fry were released unmarked (Jones et al. 2014) and suspected hatchery origin parr captured during electrofishing surveys were determined through observations made by field staff of fin erosion or condition. Between 1999 and 2006, most fall fingerlings released were adipose clipped and there were fewer unfed fry releases, thereby making the identification of wild parr easier and more accurate. From 2008 onwards, unclipped hatchery origin parr were determined by field staff based on fin erosion or condition.

The number of sites electrofished has varied from year-to-year. Variation in sample locations can bias the resulting density estimates if the proportions of high and low density sites change annually or systematically over time, and this in turn can bias survival estimates (Gibson et al. 2008b). Therefore, a generalized linear model (GLM) was used to reduce overall variation in the

time series of estimated age-class densities, and to investigate how such variation in sample locations influences the predictive capacity of juvenile data. Following the approach in Gibson et al. (2008b), mean density of a given age class was estimated for each year using 'site' and 'year' as factors in the GLM, assuming a Poisson error distribution. Gibson et al. (2008b) found that the standardized data provided better estimates of survival and a significantly better model fit when modeling the dynamics of Tobique River Atlantic Salmon using methods similar to those presented here, a result consistent with those of Gibson and Bowlby (2013) for the LaHave River (above Morgans Falls) and the St. Mary's River (West Branch) Atlantic Salmon populations. The standardized and un-standardized electrofishing time series are provided in Table A2.8. Initial model explorations indicated that using the standardized series consistently provided a better model fit than when the un-standardized series was used, so in the model runs below, only results with the standardised series are presented.

A2.2 Model Formulations

The model was set up using data from 1970 to 2011. The estimated demographic parameters for the freshwater production model are listed in Table A2.9. These include the annual mortality rates of eggs and parr (M_{Egg} and M_{Parr}), the maximum rate of population increase for age 1 parr

(α), the carrying capacity for age 1 parr (R_{asy}), and the smoltification probability at age-2 (j_2).

Similar to the analysis for the Tobique River (Gibson et al. 2009), the annual egg deposition was estimated, and a step function was used to split the model into two parts so that changes in freshwater productivity could be evaluated (the timing of the split was evaluated by profiling over the years to find the most probable split). Using the step function, reasonable model fits and parameter estimates could not be obtained. In particular, R_{asy} for the recent period could not be

estimated when abundance is low (this is evident in Model 2, see below). In addition, when profiling over the years to find the most probable break year, the 1999 consistently was identified as the most probable year, which is problematic because there would only be one year in the earlier time period for which smolt data would be available if this year was chosen.

Consistent with Gibson et al. (2009) and Gibson et al. (2013), estimating the annual egg depositions, rather than using the data as constants in the model, improved the model fit.

The relative contribution of each likelihood to the objective function value (OFV) can be controlled using a set of weighting values. These values may be selected to keep any one part of the objective function from dominating the fit, or alternatively, to reflect perceptions of data accuracy (Merritt and Quinn 2000). For the base model for the Nashwaak River population, all weights were set equal to one, an approach that has the advantage that the OFV can be interpreted as the likelihood.

A base model run was selected that consisted of using the standardized electrofishing time series and estimating a single set of parameters considered representative of the average dynamics of the entire time period. Examples of other model runs are shown in Table A2.9, including:

- 1. Model 2: similar to the base model but attempting to use a step function to estimate separate parameter values for two time periods carrying capacity (R_{asy}) could not be estimated for the more recent time period using this approach;
- 2. Model 3: similar to Model 2 with separate model parameters for the two time periods except for R_{asy} for which a single value was estimated standard errors were larger this run than for other runs, otherwise a plausible model but with limited smolt data for fitting in the earlier time period;

- 3. Model 4: similar to Model 3 but with greater weight placed on fitting to the egg and smolt time series carrying capacity could not be estimated with this formulation;
- Model 5: similar to Model 3 but with lesser weight placed on fitting to the egg and smolt time series – plausible model but with limited smolt data for fitting in the earlier time period;
- 5. Model 6: using only data from 1996 to 2011 unable to estimate carrying capacity.

Several other data combinations and likelihood weighting combinations were evaluated as well. Although the parameter estimates varied slightly in each case, none of these other model runs altered the conclusion that the dynamics exhibited in the base model are a reasonable approximation of the dynamics of the Nashwaak River population at this time.

A2.3. Results

Parameter estimates from the model are given in Table A2.9 and model fits and diagnostic plots for the base model are shown in Figure A2.1 to A2.9. Overall, the model fits to the data appear reasonable and, in the case of the base model, the parameter estimates are plausible. Fits to both the egg deposition data and the smolt counts (Figure A2.1) and to the electrofishing data (Figure A2.2) capture the general pattern in the data. The estimated abundance of smolts in the 1970's and 1980's is 2 to 5 times the estimated smolt abundance in the late-2000's. Scatterplots of the abundance of parr within a cohort in sequential age classes (Figure A2.3) illustrate the asymptotic behaviour (characteristic of density dependence) for age-1 at relatively low densities of both age-0 and age-1 fish. Although the estimated relationships appear to characterize the overall pattern in the data reasonably, the data do show scatter around the fitted relationships. Additionally, there are negative residuals at higher abundance for both the age-0 and age-2+ age classes, potentially indicating that density dependence could be occurring in more age classes than just between age-0 and age-1.

The observed and estimated return rates of 1SW and 2SW salmon to the river mouth are shown in Figure A2.4. The differences between the estimated rates and the observed rates result only from the different smolt abundance values (observed versus estimated) going into the model because the number of adults is the same in the both cases. The return rates for 1SW salmon declined during the late-1970's and 1980's, but have increased to higher levels during the 2000's. In contrast, return rates for 2SW salmon have not increased to the same extent as for 1SW salmon. Return rates to spawning escapement (Figure A2.5) were lower than to the river mouth in the earlier time periods, showing the effect of retention recreational fisheries, but the rates are more similar in recent years. However, the magnitude of the difference in the return rates to the river mouth and to spawning escapement depends on the assumed exploitation rates used to estimate past abundance, a model assumption rather than an analytical result.

MCMC diagnostic plots for estimated and derived model parameters are shown in Figures A2.6 to A2.9. In general, the trace plots (second column from left) appear reasonable, and do not show significant autocorrelation (third column from left). Minima appear reasonably defined by the OFV for all model parameters (right columns). The comparisons of the marginal probability densities with the maximum likelihood estimates (left columns) indicate very good agreement between these measures of central tendency.

Maximum lifetime reproductive rates are relatively similar among model runs (Table A2.9). For the 1970's, the estimated rates vary from a value of 1.67 to 2.74 spawners per spawner. For the 2000's, they vary from 1.03 to 1.33. The lowest value came from Model 2, in which freshwater parameter values were allowed to change once through time. All values are low enough that populations would have little to no capacity to compensate for the effects of environmental perturbations (floods, droughts, years of lower at-sea survival), leading to the conclusion that

this population is expected to extirpate in the absence of human intervention or environmental change.

Overall, the base model produces parameter estimates than are roughly similar to the parameter values produced by the other five model runs shown here (Table A2.9). One potentially important difference is that Model 1 has a higher mortality estimate for eggs and a lower mortality estimate for older parr than the other models, suggesting that the timing of mortality is earlier than that suggested by the other models. Although cases could be made to select Model 2 or Model 5 as the base model, Model 1 was choosen as the base model primarily because of the limited smolt abundance data in the earlier time period, but also because the parameter estimates are fairly similar, particularly when rolled up to the egg-to-smolt or maximum lifetime reproductive rate levels.

Further discussion of the parameter values and their implications for recovery planning is provided in the main body of the text (Sections 2.2. and 2.5).

Table A2.1. Recreational catches for the Nashwaak River. Effort data is estimated from provincial licenses. Small (1984-97) and large released (1990-94) catch data have adjusted using previous ratios of DFO officer/Prov stats from 1984-1989.

								Effort
		Catch	Retained	Released	Catch	Retained	Released	(rod
Year	Season	(small)	(small)	(small)	(large)	(large)	(large)	days)
1970	open	811	811	0	854	854	0	5,967
1971	open	733	733	0	205	205	0	4,171
1972	open	581	581	0	926	926	0	5,843
1973	open	408	408	0	923	923	0	8,597
1974	open	495	495	0	433	433	0	6,345
1975	open	663	663	0	467	467	0	8,985
1976	open	1,746	1,746	0	941	941	0	10,293
1977	open	1,096	1,096	0	1,190	1,190	0	12,062
1978	open	451	451	0	511	511	0	11,625
1979	open	960	960	0	221	221	0	9,843
1980	open	1,107	1,107	0	1,183	1,183	0	14,659
1981	open	1,085	1,085	0	498	498	0	12,896
1982	open	1,278	1,278	0	792	792	0	19,287
1983	open	420	420	0	260	260	0	14,340
1984	open	439	434	5	410	0	410	6,339
1985	open	719	654	65	673	0	673	3,233
1986	open	982	751	231	750	0	750	8,995
1987	open	886	750	136	177	0	177	6,282
1988	open	249	201	48	190	0	190	6,687
1989	open	465	448	17	214	0	214	9,335
1990	open	206	196	10	298	0	298	12,218
1991	open	228	186	42	248	0	248	12,254
1992	open	535	426	109	278	0	278	13,429
1993	open	213	137	76	82	0	82	9,063
1994	open	22	0	22	12	0	12	1,496
1995	open	n/a	0	n/a	0	0	0	11
1996	closed	0	0	0	0	0	0	n/a
1997	open	14	0	14	0	0	0	224
1998	closed	0	0	0	0	0	0	n.a.
1999	closed	0	0	0	0	0	0	n.a.
2000	closed	0	0	0	0	0	0	n.a.
2001	closed	0	0	0	0	0	0	n.a.
2002	closed	0	0	0	0	0	0	n.a.
2003	closed	0	0	0	0	0	0	n.a.
2004	closed	0	0	0	0	0	0	n.a.
2005	closed	0	0	0	0	0	0	n.a.
2006	closed	0	0	0	0	0	0	n.a.
2007	closed	0	0	0	0	0	0	n.a.
2008	closed	0	0	0	0	0	0	n.a.
2009	closed	0	0	0	0	0	0	n.a.
2010	closed	0	0	0	0	0	0	n.a.
2011	closed	0	0	0	0	0	0	n.a.

Table A2.2. Proportions of wild origin adult Atlantic Salmon that are virgin one sea-winter (1SW), virgin two sea-winter (2SW), and repeat spawning salmon based on samples collected at a counting fence on the Nashwaak River for three years in the 1970's and from 1993 to 2011. The proportion of 2SW salmon in the large component of the population, used to split the large component of the recreational catch in the population model, is also shown.

		Proportion			
Year	Total abundance	1SW	2SW	Repeat spawners	2SW in the large component
1972	3,095	0.344	0.622	0.031	0.948
1973	4,093	0.234	0.628	0.130	0.819
1975	2,969	0.541	0.377	0.065	0.822
1993	1,233	0.672	0.224	0.090	0.682
1994	972	0.635	0.291	0.074	0.797
1995	1,315	0.684	0.302	0.015	0.954
1996	2,223	0.738	0.204	0.058	0.779
1997	671	0.495	0.422	0.083	0.836
1998	1,552	0.809	0.122	0.069	0.639
1999	936	0.706	0.199	0.085	0.677
2000	701	0.726	0.217	0.052	0.794
2001	513	0.472	0.463	0.065	0.877
2002	415	0.824	0.109	0.067	0.621
2003	396	0.725	0.250	0.026	0.907
2004	777	0.739	0.244	0.018	0.932
2005	856	0.814	0.166	0.020	0.892
2006	852	0.777	0.204	0.019	0.917
2007	561	0.822	0.141	0.037	0.793
2008	1,384	0.876	0.114	0.009	0.926
2009	607	0.465	0.448	0.087	0.837
2010	2,166	0.911	0.069	0.020	0.779
2011	1,544	0.637	0.341	0.022	0.938

Table A2.3. Spawning escapement for 1SW and multi sea-winter (MSW) Atlantic Salmon, and the egg deposition time series used for inputs for the Nashwaak River population dynamics models. The proportion of the MSW salmon component (which includes repeat-spawners) that are 2SW salmon, and the proportions of 1SW and MSW salmon that are of wild origin based on sampling of the adult population, are also shown.

				Proportions		
			Egg	2SW in	1SW	
			deposition	MSW	that are	MSW that
Year	1SW	MSW	(millions)	component	wild	are wild
1970	1,312	1,402	9.606	0.863	1.000	1.000
1971	1,186	337	2.960	0.863	1.000	1.000
1972	624	964	9.957	0.948	1.000	1.000
1973	1,039	2,533	15.190	0.819	1.000	1.000
1974	801	711	4.972	0.863	1.000	1.000
1975	1,072	767	5.520	0.822	1.000	1.000
1976	2,824	1,545	11.620	0.863	1.000	1.000
1977	1,773	1,954	13.344	0.863	1.000	1.000
1978	729	839	5.706	0.863	0.992	1.000
1979	1,553	363	3.397	0.863	0.970	0.993
1980	1,790	1,942	13.287	0.863	0.905	0.981
1981	1,755	818	6.345	0.863	0.939	0.947
1982	2,067	1,300	9.547	0.863	0.980	0.974
1983	679	427	3.135	0.863	0.861	0.964
1984	702	1,067	7.264	0.820	0.836	0.899
1985	1,058	1,751	11.792	0.820	0.874	0.937
1986	1,215	1,951	13.191	0.820	0.952	0.957
1987	1,213	461	4.409	0.820	0.974	0.888
1988	325	494	3.366	0.820	0.887	0.973
1989	725	557	4.293	0.820	0.963	0.947
1990	317	775	5.010	0.820	0.984	0.976
1991	301	645	4.221	0.820	0.887	0.994
1992	689	723	5.224	0.820	0.953	0.970
1993	866	555	3.948	0.682	0.868	0.730
1994	610	349	3.264	0.797	0.933	0.915
1995	940	436	4.222	0.954	0.956	0.954
1996	1,804	641	6.203	0.779	0.897	0.887
1997	364	362	2.888	0.836	0.897	0.926
1998	1,238	309	3.917	0.639	0.998	0.940
1999	658	269	2.468	0.677	0.994	1.000
2000	489	189	1.887	0.794	1.000	1.000
2001	224	266	2.034	0.877	0.992	0.996
2002	320	69	0.725	0.621	0.997	0.924
2003	280	109	0.950	0.907	0.966	0.965
2004	569	201	2.116	0.932	0.973	0.981
2005	712	155	2.007	0.892	0.953	0.981
2006	681	186	2.045	0.917	0.925	0.974
2007	442	98	1.166	0.793	0.983	0.943
2008	1,217	168	2.932	0.926	0.981	0.988
2009	274	328	1.780	0.837	0.949	0.967
2010	2,008	195	3.942	0.779	0.979	0.980
2011	1,033	575	4.739	0.938	0.951	0.974

Table A2.4. Average probabilities that 1SW and 2SW salmon return to spawn as either alternate-year or consecutive-year repeat spawners for a second or third spawning event based on biological data corresponding to cohorts spawning for the first time in the years 1993 to 2009.

Variable	Probabilities				
To a second spawning:					
$P_{1,alt}$	0.023				
$p_{1,cons}$	0.008				
$p_{2,alt}$	0.046				
$p_{2,cons}$	0.044				
To a third spawning:					
$P_{1,alt,alt}$	0.000				
$P_{1,alt,cons}$	0.108				
$p_{1,cons,alt}$	0.000				
$P_{1,cons,cons}$	0.072				
$p_{2,alt,alt}$	0.202				
$p_{2,alt,cons}$	0.046				
$p_{2,cons,alt}$	0.113				
$p_{2,cons,cons}$	0.031				
Table A2.5. Mean fork length, proportion female and estimated fecundity for 1SW and MSW Atlantic Salmon in the Nashwaak River based on samples collected at the counting fence. Expected number of eggs per fish (sexes combined) for each age class during two time periods are also shown.

Voor	Mean Fork Length (cm)		Proportion	Female	Estimated Fecundity	
real	1SW	MSW	1SW	MSW	1SW	MSW
1972	57.5	76.3	0.328	0.822	3,419	6,733
1973	54.7	78.2	0.212	0.835	3,091	7,211
1975	55.1	79.3	0.152	0.918	3,136	7,503
Mean:	55.8	77.9	0.231	0.858	3,215	7,149
1993	57.1	77.8	0.279	0.858	3,370	7,108
1994	58.8	78.7	0.517	0.850	3,583	7,342
1995	57.2	78.3	0.363	0.983	3,382	7,237
1996	57.1	78.7	0.437	0.759	3,370	7,342
1997	57.0	79.8	0.440	0.861	3,358	7,639
1998	57.0	80.4	0.518	0.723	3,358	7,806
1999	58.4	79.8	0.459	0.679	3,532	7,639
2000	56.9	79.8	0.360	0.899	3,346	7,639
2001	58.4	78.1	0.393	0.900	3,532	7,185
2002	57.7	82.2	0.304	0.672	3,444	8,329
2003	58.1	77.5	0.273	0.900	3,494	7,031
2004	58.2	78.7	0.440	0.852	3,506	7,342
2005	57.8	78.3	0.433	0.862	3,456	7,237
2006	57.4	79.9	0.410	0.780	3,407	7,667
2007	57.7	79.1	0.419	0.747	3,444	7,449
2008	57.7	77.2	0.496	0.736	3,444	6,956
2009	56.9	77.0	0.289	0.663	3,346	6,906
2010	57.0	77.7	0.440	0.702	3,358	7,082
2011	57.8	79.5	0.478	0.707	3,456	7,557
Mean:	57.6	78.9	0.408	0.796	3,431	7,394

Table A2.6.Expected number of eggs per fish (sexes combined) for one 1SW and MSW Atlantic Salmon in the Nashwaak River for two time periods are also shown. Values are calculated using the mean values shown in Table A2.5.

Age group	Time period	Expected number of eggs
1SW	1970's	742
1SW	1993 - 2011	1,399
MSW	1970's	6,136
MSW	1993 - 2011	5,890

	Abundance	Number	Number	Number	Number
Year	estimate	sampled	age-2	age-3	age-4
1998	22,750	204	162	42	0
1999	28,500	287	193	87	7
2000	15,800	208	117	89	2
2001	11,000	194	166	28	0
2002	15,000	230	209	21	0
2003	9,000	137	103	34	0
2004	13,600	154	118	36	0
2005	5,200	59	35	24	0
2006	25,400	401	340	61	0
2007	21,550	343	301	42	0
2008	7,300	359	265	94	0
2009	15,900	420	353	67	0
2010	12,500	426	221	205	0
2011	8,750	166	136	30	0
2012	11,060	154	93	61	0

Table A2.7. Smolt abundance in the Nashwaak River from 1998 to 2012; and the number of smolts sampled by age class.

Table A2.8. Annual mean densities of juvenile Atlantic Salmon by age class in the Nashwaak River used as inputs for the population dynamics model. Two variants of the data are used: "Un-standardized" values are annual means calculated directly from the data, whereas the "Standardized" values are estimated with a generalized linear model with "site" and "year" as factors to correct for the effects of changes in the sites included in the survey each year.

		Un-standardized			Standardized		
Year	Ν	Age-0	Age-1	Age-2	Age-0	Age-1	Age-2
1970	3	15.00	3.83	7.03	18.86	3.49	7.66
1971	10	46.35	5.72	7.07	46.35	5.72	7.07
1972	10	21.00	1.82	13.82	21.00	1.82	13.82
1973	10	27.33	0.09	10.17	27.33	0.09	10.17
1974	10	54.54	1.88	8.88	54.54	1.88	8.88
1975	10	50.64	14.05	9.52	50.64	14.05	9.52
1976	10	33.86	7.94	2.16	33.86	7.94	2.16
1977	10	24.75	10.87	2.21	24.75	10.87	2.21
1978	8	48.86	6.85	3.53	46.65	6.86	3.49
1979	5	71.96	16.04	4.42	47.18	13.78	4.55
1981	7	53.71	14.17	4.21	44.78	11.57	3.49
1982	8	40.45	9.88	2.99	37.56	9.12	2.79
1983	8	20.76	7.83	2.91	19.28	7.23	2.72
1984	8	33.69	5.38	1.85	31.28	4.97	1.73
1985	8	35.30	6.29	2.56	32.78	5.81	2.39
1986	8	38.64	7.06	2.09	35.87	6.52	1.95
1987	8	52.40	11.70	0.78	48.65	10.81	0.72
1988	8	48.25	9.80	1.06	44.80	9.05	0.99
1989	8	46.39	11.35	1.91	43.07	10.49	1.79
1990	8	33.61	10.49	1.64	31.21	9.69	1.53
1991	8	32.46	8.68	1.51	30.14	8.01	1.41
1992	9	26.70	12.90	1.04	24.31	11.85	0.96
1993	9	12.72	7.00	1.98	11.58	6.43	1.83
1994	10	3.99	3.29	0.76	3.99	3.29	0.76
1995	8	10.46	8.64	1.58	9.71	7.98	1.47
1996	9	8.10	3.31	0.63	8.35	3.36	0.65
1997	9	12.93	5.33	0.86	13.33	5.42	0.87
1998	10	3.61	3.85	0.98	3.61	3.85	0.98
1999	10	7.91	4.37	1.18	7.91	4.37	1.18
2000	9	11.83	4.02	0.10	12.20	4.09	0.10
2001	9	11.92	9.38	1.19	10.85	8.61	1.10
2002	8	15.43	5.51	1.26	14.32	5.09	1.18
2003	9	4.79	5.01	0.72	4.36	4.60	0.67
2004	9	5.21	2.41	0.67	4.74	2.21	0.62
2005	9	6.79	4.49	0.42	6.18	4.12	0.39
2006	8	3.03	4.64	0.71	2.97	3.81	0.59
2007	9	5.53	4.04	0.50	5.04	3.71	0.46
2008	9	8.02	4.86	0.89	7.30	4.46	0.82
2009	9	6.04	2.89	0.64	5.50	2.65	0.59
2010	9	19.58	4.74	0.96	17.82	4.36	0.88
2011	8	2.33	4.79	0.49	1.92	3.94	0.40

Table A2.9. Maximum likelihood estimates (standard errors) for life history parameter estimates for the Nashwaak River Atlantic Salmon population obtained from six versions of the dynamics model. The objective function value (OFV) for Model 6 is not comparable to others because the data series is shorter; similarly the OFV for models 4 and 5 are not comparable to the others because of the weights. "NA" values occur where a model parameter is not applicable (e.g. if only a single survival is estimated as in models without a break year). "Past" dynamics are those for the 1973-82 cohorts, whereas "present" refers to the 2000-09 cohorts, except in models without a break year in which the "past" estimates are used for the full time period.

Model:	Base	Model 2	Model 3	Model 4	Model 5	Model 6		
Assumptions and Fit:								
Time period:	1970-2011	1970-2011	1970-2011	1970-2011	1970-2011	1993-2011		
Standardized electrofishing								
data:	yes	yes	yes	yes	yes	yes		
Break year	None	1999	1999 but 1 Rasy	1999 but 1 Rasy	1999 but 1 Rasy	None		
Weights: eggs, smolt, smolt age	1	1	1	10	1/10	1		
OFV	719.5	697.3	698.5	7,312.5	0.42	2,165.4		
Freshwater production:								
Electro a	10,044 (2,929)	17,376 (4,733)	17,562 (4,813)	17,795 (3,937)	17,845 (7,972)	17,009 (5,567)		
M_{Egg} (past)	0.96 (0.01)	0.94 (0.02)	0.94 (0.02)	0.94 (0.01)	0.93 (0.04)	0.95 (0.02)		
M_{Egg} (present)	ŇAÚ	0.93 (0.02)	0.93 (0.02)	0.91 (0.02)	0.94 (0.03)	ŇA		
α (past)	0.54 (0.07)	0.44 (0.09)	0.36 (0.07)	0.38 (0.04)	0.49 (0.12)	0.63 (0.07)		
α (present)	NA	0.62 (0.08)	0.65 (0.1)	0.53 (0.06)	0.79 (0.15)	NA		
R_{asy} (past)	28.01 (8.79)	28.2 (28.2)	69.427 (95)	infinite	20.143 (8)	infinite		
R _{asy} (present)	NÀ	infinite	NA	NA	NA	NA		
M_{Parr} (past)	0.53 (0.1)	0.59 (0.08)	0.58 (0.08)	0.61 (0.06)	0.59 (0.15)	0.70 (0.07)		
M_{Parr} (present)	NÀ	0.73 (0.06)	0.73 (0.06)	0.75 (0.04)	0.73 (0.07)	NA		
j_2 (past)	0.61 (0.06)	0.49 (0.07)	0.5 (0.07)	0.47 (0.05)	0.50 (0.16)	0.5 (0.06)		
j_2 (present)	ŇA	0.49 (0.05)	0.49 (0.05)	0.47 (0.04)	0.48 (0.08)	ŇA		
j_3 (past)	0.99 (0.01)	0.91 (0.04)	0.50 (0.07)	0.90 (0.02)	0.91 (0.01)	0.98 (0.01)		
j₃ (present)	NA	1.00 (<0.01)	1.00 (<0.01)	1.00 (<0.01)	1.00 (<0.01)	NA		
Egg to smolt dynamics:								
$\breve{\alpha}$ (past)	0.007 (0.001)	0.008 (0.002)	0.007 (0.002)	0.005 (0.001)	0.01 (0.006)	0.006 (0.001)		
$\breve{\alpha}$ (present)	NA	0.007 (0.001)	0.007 (0.001)	0.007 (0)	0.009 (0.004)	NA		
\breve{R}_{asy} (past) (thousands)	104.4 (36.2)	140.1 (84.5)	353.2 (499.7)	infinite	101.3 (70.9)	infinite		
\breve{R}_{asy} (present) (thousands)	NA	infinite	206.0 (282.8)	Infinite	61.2 (30.5)	NA		

		1				1		
Model:	Base	Model 2	Model 3	Model 4	Model 5	Model 6		
Return Rates (%):								
1SW average (past) 1SW average (present) 2SW average (past) 2SW average (present)	6.18 (0.85) 4.95 (0.45) 4.04 (0.56) 1.10 (0.1)	5.27 (1.34) 5.02 (0.48) 3.44 (0.87) 1.11 (0.11)	4.84 (1.27) 5.00 (0.48) 3.20 (0.84) 1.11 (0.11)	5.53 (0.58) 4.97 (0.16) 3.73 (0.38) 1.12 (0.04)	5.22 (3.22) 5.23 (1.54) 3.36 (2.1) 1.11 (0.33)	NA NA NA NA		
Lifetime egg prod. per smolt:	, , , , , , , , , , , , , , , , , , ,			~ /		1		
average EPS (past) average EPS (present)	333.2 (45.8) 150.9 (13.7)	284.1 (72.2) 153 (14.7)	263.4 (69.0) 152.4 (14.7)	306.4 (31.5) 152.8 (4.8)	278.3 (173.1) 156.06 (45.7)	NA NA		
Max. lifetime reproductive rate:								
average (past) average (present)	2.49 (0.42) 1.13 (0.12)	2.3 (0.58) 1.03 (0.11)	1.79 (0.42) 1.11 (0.15)	1.67 (0.16) 1.09 (0.06)	2.74 (0.97) 1.33 (0.43)	NA NA		
Equi. egg abundance (millions):								
average (past) average (present)	20.81 (4.04) 1.76 (1.13)	22.49 (7.28) infinite	41.41 (43.96) 3.17 (3.33)	infinite infinite	17.90 (5.90) 2.39 (2.21)	NA NA		
Equi. Smolt abundance (thousands):								
average (past) average (present)	62.4 (15.9.) 11.6 (7.4)	79.2 (35.0) infinite	156.2 (179.90) 20.8 (21.9)	infinite infinite	64.3 (41.1) 15.3 (14.8)	NA NA		



Figure A2.1. Observed (points) and estimated (solid lines) egg depositions (top panel) and smolt counts (bottom panel) from the base population dynamics model for the Nashwaak River Atlantic Salmon population. The dashed lines show 95% confidence intervals based on normal approximations.



Figure A2.2. Observed (points) and estimated (solid lines) age-0 (top panel), age-1 (middle panel) and age-2+ (bottom panel) juvenile salmon densities from the base population dynamics model for the Nashwaak River Atlantic Salmon population. The dashed lines show 95% confidence intervals based on normal approximations.



Figure A2.3. Functional relationships between the abundance of eggs, and the densities of age-0, age-1 and age-2+ juvenile salmon from the base population dynamics model for the Nashwaak River Atlantic Salmon population. The points show the data and the lines show the fitted relationships between age classes.



Figure A2.4. Observed (points) and estimated (solid lines) smolt-to-adult return rates to the river mouth (indicative of at-sea survival) for salmon returning as one sea-winter (top panel) and two sea-winter (bottom panel) adults. Estimates are obtained from the base population dynamics model for the Nashwaak River Atlantic Salmon population. The dashed lines show 95% confidence intervals based on normal approximations.



Figure A2.5. Estimated (solid lines) smolt-to adult return rates to spawning escapement (includes the effects of both at-sea survival and the recreational fishery) for salmon returning as one sea-winter (top panel) and two sea-winter (bottom panel) adults. Estimates are obtained from the base population dynamics model for the Nashwaak River Atlantic Salmon population. The dashed lines show 95% confidence intervals based on normal approximations.



Figure A2.6. Markov Chain Monte Carlo (MCMC) results for the freshwater production model survival parameters for the Nashwaak River base model run. The first column shows the probability density (the dashed lines are the maximum likelihood estimates), the second column shows the thinned chain, the third column shows the auto-correlation in the chain, and the fourth column is a plot of the objective function value versus the parameter value for each step in the MCMC chain.



Figure A2.7. MCMC results for two derived model parameters for the Nashwaak River base model run: the egg-to-smolt Beverton-Holt alpha and asymptotic recruitment level and the mean lifetime egg-per smolt values for. A single set of two estimated values were used for the entire time period. The first column shows the probability density (the dashed lines are the maximum likelihood estimates), the second column shows the thinned chain, the third column shows the auto-correlation in the chain, and the fourth column is a plot of the OFV versus the parameter value for each step in the MCMC chain.



Figure A2.8. MCMC results for three derived model parameters (mean lifetime egg production per smolt (EPS) and the equilibrium abundance of eggs) for two time periods (start = 1973-1982; end = 2000-2009) for Nashwaak River base model. The first column shows the probability density (the dashed lines are the maximum likelihood estimates), the second column shows the thinned chain, the third column shows the auto-correlation in the chain, and the fourth column is a plot of the OFV versus the parameter value for each step in the MCMC chain.



Figure A2.9. MCMC results for two derived model parameters (mean equilibrium abundance of smolts, and maximum lifetime reproductive rate) for two time periods (start = 1973-1982; end = 2000-2009) for Nashwaak River base model. The first column shows the probability density (the dashed lines are the maximum likelihood estimates), the second column shows the thinned chain, the third column shows the auto-correlation in the chain, and the fourth column is a plot of the OFV versus the parameter value for each step in the MCMC chain.

APPENDIX 3. DESCRIPTION OF MODELS USED FOR THE POPULATION VIABILITY ANALYSES FOR OUTER BAY OF FUNDY ATLANTIC SALMON

The following text is slightly modified from Gibson and Bowlby (2013).

The population viability analyses presented in Sections 3 and 4 were carried out using a forward projecting population model developed specifically for the life history of Outer Bay of Fundy Atlantic Salmon. Population viability analysis (PVA) is a powerful tool to explore current conditions, assess risks and simulate how future management actions or environmental changes could influence the abundance of a population (Reed et al. 2002). The dynamical model (i.e. describing the life history) is identical to the one described in Appendix 1, with a slight variation in that all repeat spawning salmon are assumed to be consecutive year spawners after their second spawning (they may be alternate or consecutive year spawners between their first and second spawning). This variation has very little effect on the model output because it only slightly modifies the probability of surviving between spawning events and very, very few salmon survive to spawn a third time.

The dynamical equations used to project the population forward through time are the same as those for the life history model presented in Appendix 1, with the addition of random variability in survivals and stage transition probabilities (described below). A starting abundance equal to the average population size for the years 1997 to 2011 are used to initialize the model.

Two sets of life history parameter values are used in the simulations: those that are representative of the 1973 to 1982 cohorts (past dynamics) and those that are representative of the 2000 to 2009 cohorts (present dynamics). These values are those estimated using the statistical model and are provided in Section 2.

For both the past and present scenarios, the numbers of eggs, parr, smolt and adults, as well as their age, sex and previous spawning structure, are calculated using the mean life history parameter values specific to the simulation, corresponding to the starting population size.

Random variability was incorporated into future mortality rates, sex ratio, and maturity schedules for greater biological realism (Shelton et al. 2007). A lognormal distribution was used for the deviates around the mortality parameters (or functions), and a logistic distribution for the probabilities of smoltification, the proportion maturing after one winter or two winters at sea and the probability of being a consecutive or alternate year repeat spawner, as well as the sex ratio parameters. Lognormal distributions are often used to model the deviates around survival functions as survival is multiplicative in nature. Given that sex ratio and maturity are proportions, the logistic transformation better describes the binomial nature of their error distributions.

Deviates are expected to be temporally autocorrelated (Hilborn 2001) given that the effect of environmental variability on population vital rates tends not to be completely random (Lande et al. 2003). As the strength of this autocorrelation increases, good years are increasingly likely to be followed by good years (and bad followed by bad).

Example of how lognormal variability in survival parameters was incorporated:

Let \overline{M} equal the average instantaneous rate of mortality affecting a life stage of salmon (as estimated using the life history model), σ_w equal the standard deviation of the residuals of the

mortality rate (the amount of variability in the rate) and d be a constant describing the degree of autocorrelation. The instantaneous mortality used in the forward projection in year t is given by:

$$M_t = \overline{M} + w_t + \sigma_w^2 / 2$$

where

$$w_t = (w_{t-1}^* d + w_t^*)\sigma_w$$

and

$$w_{t}^{*} \sim N(0,1).$$

The parameter M_{t} is then used to model the survival between 2 ages, following the general format of:

 $N_{t+1} = N_t \exp(-M_t)$

Note that although the survival estimated by this algorithm is not strictly bounded to fall below one, for practical purposes it meets this criterion given the rates used in this analysis. In multiple model runs of 2000 simulated populations, each with several life history parameters, at no time was a survival value greater than one simulated with this algorithm.

For the population projection model used in the PVA (above), the random variability in the egg, parr and mature salmon mortality parameters M_t^{Egg} , M_t^{Parr} , M_t^{Mat} were modeled in this fashion after converting the annual mortality rates estimated with the statistical model to instantaneous rates. Additionally, the return rates for 1SW and 2SW salmon were converted to instantaneous mortality rates and modeled similarly, and random variability was included around the age-0 to age-1 survival function in the same way.

Example of how logistic variability was incorporated into stage transition probabilities and sex ratios:

Let p be the mean parameter value in the form of a proportion. The logit mean of the parameter (S) becomes:

$$S = \ln(p/(1-p))$$

Autocorrelated random deviates for t years are calculated as:

$$w_t = (w_{t-1}^* d + w_t^*) \sigma_w$$

where

$$w_{t}^{*} \sim N(0,1)$$

where d and σ_w are as described above.

The annual probability becomes:

$$p_t = \exp(S + w_t) / (1 + \exp(S + w_t))$$

where p_t is the probability of transitioning from one life stage to another (e.g. smolting or not smolting at a given age, maturing or not maturing at a given age, etc.) in the given year.

Random variability and autocorrelation:

The values used for random variability and autocorrelation are those used by Gibson and Bowlby (2013). Based on their analysis of autocorrelation in the return rate time series for the LaHave River and St. Mary's River populations, the autocorrelation coefficient in the marine environment was set to 0.45, and a (instantaneous) return rate variance of 0.475 was used for the PVA's. The same autocorrelation coefficient value was assumed for the freshwater environment as was derived for the marine environment. However, random variability was assumed to be lower in the freshwater environment and values of $\sigma = 0.2$ were assumed for all other model parameters, except for the probability of smoltification for which a value of 0.3 was assumed. Within limits, the general extinction patterns are not overly sensitive to perturbations of the variances (i.e. higher or lower values for σ), although the time to extinction does vary as more or less variability is assumed. Examples of a simulated mortality rate and smoltification probability time series are shown in Figures A3.1 and A3.2 to illustrate how mortality varies in the PVA. Note that, because the same random numbers are used to generate the series, the pattern is the same for each parameter, but the values are re-scaled by the average rates.

Catastrophic events:

Atlantic Salmon occupy naturally variable habitats that are at times subject to extreme conditions. Floods and droughts in fresh water are examples of these, both of which can lead to very high mortality in one or many of the juvenile life stages. The effects of extreme events are included in the model using two parameters. The first parameter is the frequency parameter, ψ ,

which is the expected number of these events in 100 years. A random number, v_t , is drawn from a uniform distribution [0,1] for each year in each simulated population trajectory, and the value $1/\psi$ is compared to v_t . If $v_t < 1/\psi$, that year is considered an extreme event year. The second parameter, ϑ , is used to model the effect of the event. In this analysis, the effect of the event was included between the egg and the fry life stages, thereby allowing density-dependent compensation to occur which would partially offset some of the mortality (because the survival of age 0 to age 1 increases as population size decreases). The effect of the events would be greater if it was incorporated after density dependence. The simulated number of fry, $P_{t,0}$, is then:

$$P_{t,0} = \left\langle \begin{array}{ccc} Egg_t e^{-M_t^{Egg}} \mathcal{G} & \text{if } \upsilon_t < 1/\psi, \quad \upsilon_t \sim \text{unif}[0,1] \\ Egg_t e^{-M_t^{Egg}} & \text{otherwise} \end{array} \right\rangle$$

In the absence of specific information about the frequency and effects of extreme events, values of 10 and 0.2 were assumed for ψ and ϑ , respectively. This means that on average, 10 events reducing the abundance of fry by 80% from the expected value would occur every 100 years. As modeled, a greater or lesser number of extreme events could occur in any simulated population trajectory, and their distribution through time is random. To illustrate the effects of including extreme events, 1000 random survival values were generated assuming a mean survival of 0.5 and $\sigma = 0.2$. These values are compared to a set of random survivals including catastrophic events assuming values of 10 and 0.2 for ψ and ϑ , respectively (Figure A3.3). In this example, the median survival is reduced from 0.488 to 0.476 when extreme events are included.

Probability of extinction and recovery:

For each scenario analyzed with the PVA, 2000 population trajectories were simulated and the extinction probabilities are calculated as the proportion of populations that go extinct by a specified time. A quasi-extinction threshold of 15 females is assumed and an egg deposition of zero is assigned if the abundance drops below this value. A population must be below this value

for two consecutive years to be assumed extinct in a given year. If the female abundance is higher the next year, the egg deposition is calculated as per the model. A population can therefore sit on the quasi-extinction for a number of years and can theoretically recover. Recovery probabilities were calculated as the proportion of the simulated population trajectories that were above the recovery target in a given year. As such, a population could be in a recovered state for a period of time, and then cease to be considered recovered if its abundance subsequently declined to a level below the recovery target.

In instances where comparisons were made between scenarios, the same set of random numbers was used to generate variability in parameter values to ensure that the differences between the scenarios do not occur by chance (i.e. because a different set of numbers is used).



Figure A3.1. Examples of how the life history parameter values used change through time given the autocorrelation values and extent of random variability used in the analyses. Starting values for the parameters are from the base case population viability analysis for Nashwaak using past (1973-1982) population dynamics. Values are for a single 100-year stochastic projection.



Figure A3.2. Examples of how the life history parameter values used change through time given the autocorrelation values and extent of random variability used in the analyses. Starting values for the parameters are from the base case population viability analysis for Nashwaak River using present (2000's) population dynamics. Values are for a single 100-year stochastic projection.



Figure A3.3. Comparison of two sets of 1000 random survival values generated assuming a mean survival of 0.5 and $\sigma = 0.2$ with the distribution in the lower panel including catastrophic events. Values of 10 and 0.2 were assumed for ψ and ϑ , respectively (from Gibson and Bowlby 2013).