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Assessing allowable harm and recovery efforts in Lake Ontario Atlantic salmon (*Salmo salar*)

Évaluation des dommages admissibles et des efforts de rétablissement concernant le saumon atlantique (*Salmo salar*) du lac Ontario

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ABSTRACT

Atlantic salmon (*Salmo salar*) was extirpated from the Lake Ontario basin by the end of the 19th century. Continuous restocking attempts have been unsuccessful in establishing self-sufficient populations. We use a demographic perturbation analysis to assess the maximum allowable harm and minimum recovery efforts for Lake Ontario Atlantic salmon (LOAS). Our results indicate that (i) a recreational fishery for LOAS and management efforts to improve population performance can coexist through effective fishing regulations and recovery strategies, (ii) the most effective and feasible way of improving the population is through the survival rates of immature individuals, and (iii) catch size limits can be used as a conservative, risk-averse regulation for maximum allowable fishing mortality. This document is provided in support of a recovery potential assessment (RPA) conducted for Lake Ontario Atlantic salmon.

RÉSUMÉ

Le saumon atlantique (*Salmo salar*) a disparu du bassin du lac Ontario vers la fin du 19e siècle. Les efforts continus de réensemencement n’ont pas permis le rétablissement de populations auto-suffisantes. Nous avons utilisé une analyse de la perturbation démographique pour évaluer les dommages admissibles maximaux et les efforts de rétablissement minimaux pour le saumon atlantique du lac Ontario. Ainsi, selon nos résultats : i) il est possible, dans lac Ontario, d’avoir une pêche sportive au saumon atlantique et de consentir en même temps des efforts de gestion pour améliorer le rendement de la population par l’application d’une réglementation sur la pêche et la mise en œuvre de programmes de rétablissement efficaces; ii) le moyen le plus efficace et le plus plausible pour améliorer la population est d’augmenter le taux de survie des individus immatures; iii) on peut utiliser des limites sur la taille des prises pour assurer une gestion prudente et fondée sur le risque de la mortalité maximale permise par la pêche. Ce document est produit à l’appui d’une évaluation du potentiel de rétablissement (EPR) du saumon atlantique du lac Ontario.

INTRODUCTION

Historically, Atlantic salmon (*Salmo salar*) used many Lake Ontario tributaries for spawning and juvenile production (COSEWIC 2006). Evidence suggests that the Lake Ontario Atlantic salmon (LOAS) population was geographically and reproductively isolated from other Atlantic anadromous populations and that freshwater adults once populating Lake Ontario were smaller than anadromous strains (COSEWIC 2006). Atlantic salmon was extirpated from the Lake Ontario basin by the end of the 19th century (Parsons 1973, Scott and Crossman 1973) and continuous restocking attempts have been unsuccessful in establishing self-sustaining populations (MacKay 1963). Overfishing and habitat degradation, primarily habitat fragmentation through dams, are regarded as the most important causes of population collapse (Dunfield 1985). The Ontario Ministry of Natural Resources (OMNR) initiated an experimental program in 1987 to re-establish Atlantic salmon populations in Lake Ontario and to provide a sport fishery based on naturally reproducing populations, supplemented by stocking of hatchery-reared fish (Bisset et al. 1993). Similar efforts by the New York State Department of Environmental Conservation (NYDEC) generated a small and consistent lake fishery mostly dependent on stocking as natural reproduction was seemingly non-existent (Eckert 2003).

Commercial Atlantic salmon fisheries in Canada and the United States have been closed since 2000. Several recent watershed fisheries management plans have identified public interest in restoring naturally sustaining populations of Atlantic salmon in Lake Ontario. In addition, stocking programs have been initiated by U.S. government and non-governmental agencies in lakes Huron, Michigan, and Superior (COSEWIC 2006). The lake sport fishing season for stocked fish in Ontario is open from January 1 to September 30 with an allowable harvest of one salmon (63 cm or greater) per day per fisher; however, fishing in tributaries of Lake Ontario is closed year-round. Current restoration efforts for LOAS are consistent with a recent Biodiversity Strategy for Ontario (COSEWIC 2006).

The *Species at Risk Act* (SARA) is intended to protect species at risk of extinction or extirpation in Canada and to promote their recovery. Recovery potential assessment (RPA) plays an important role in this process and consists of three phases: species status, scope for human-induced harm (allowable harm), and mitigation (DFO 2005a, 2005b). Under SARA, an interim assessment of allowable human-induced harm is needed for the permitting of human activities until a recovery strategy is developed. The mitigation component requires the identification of recovery targets, time frame for recovery, and specification of the uncertainty of outcomes associated with management actions (DFO 2005a, 2005b). SARA does not define recovery in the Act, but expert groups should reach consensus on the biological characteristics of a population which would constitute "recovery", as a core part of science support to recovery planning (DFO 2005c). This has sometimes been difficult and remains a challenge to ensure that recovery targets are scientifically well-based.

An allowable harm analysis (AHA) provides an assessment of the level of harm that can be permitted without jeopardizing the survival or recovery of a species. Based on the framework revised by DFO (Canadian Science Advisory Secretariat 2004), AHA has been applied mainly to commercial marine species for which time series are available. Current efforts to assess allowable harm in freshwater species at risk are essentially qualitative, based mostly on expert opinion. Once a species is listed as endangered or threatened, SARA restricts harm from human activities under the conditions set out in section 73(3):

(a) all reasonable alternatives to the activity that would reduce the impact on the species have been considered and the best solution has been adopted;

(b) all feasible measures will be taken to minimize the impact of the activity on the species or its critical habitat or the residences of its individuals; and

(c) the activity will not jeopardize the survival or recovery of the species.

The function of AHA is to provide scientific advice in support of paragraph 73(3)(c) about the levels of harm a species (or population) could sustain without compromising the above conditions during the time between listing and implementation of a recovery plan.

Following an initiative to work on AHA for freshwater species at risk, Vélez-Espino and Koops (2007) developed a methodology to estimate allowable harm in species at risk with minimal demographic data. Briefly, the approach relies on demographic modelling widely applied in conservation biology (e.g., Crouse et al. 1987; Cortés 2002; Wilson 2003), resource management (e.g., Getz and Haight 1989; Hayes 2000) and pest control (Rockwell et al. 1997, Shea and Kelly 1998, Neubert and Caswell 2000), in which harm is defined as a negative perturbation that can target one or more vital rates and life stages simultaneously. This quantitative assessment of allowable harm uses perturbation analysis, a demographic prospective technique that depends on the construction of projection matrices from which population growth rate (λ) can be calculated and the relative importance of each vital rate (i.e., elasticities) can be used to project the effects of management interventions (Caswell 2000). Within this framework, allowable harm is a function of (a) the vital rate(s) impacted by human action(s), (b) the elasticities of impacted vital rate(s), (c) the population growth rate before allowing the harm, and (d) the minimum population growth rate that will not jeopardize the survival and future recovery of the population. Hence, population growth rate will be susceptible not only to human-induced mortality but also to suppression of reproductive success and growth rates caused by human actions. Additional characteristics of this approach are that it requires minimal data while using all available data, has the capability to link population dynamics with habitat-based information, is flexible enough to assess complex life histories, and follows a precautionary approach.

Part of the methodology relies on the assumption that after a species is listed as threatened or endangered protection is granted and the main causes of decline are removed. This is reasonable when anthropogenic activities directly constitute the main population stressors. However, in some cases natural and complex factors operating on temporal and spatial scales different from those of human activities can play an important role in the impairment of population dynamics. Therefore, violations of the assumption that causes of decline have been removed will compromise the validity of inferred estimates of population growth rate that are part of the AHA and likely produce falsely optimistic estimates of allowable harm (Vélez-Espino and Koops 2007). The best case scenario would be that the major causes of decline have ceased and the population growth rate is maximized, in which case AHA would be suitable. The worst case scenario would be that listing and protection does not remove population stressors and population growth remains negative. In this case, AHA must be cautiously applied, accepting the possibility that recovery strategies need to be implemented in the short term.

The DFO framework for developing science advice on recovery targets for aquatic species in the context of SARA (DFO 2005c) identified direct estimates of total population size and total range occupied as the preferred currencies for specifying recovery targets and focusing recovery efforts. Building upon the work of Vélez-Espino and Koops (2007), we introduce a dynamic currency for specifying recovery efforts based on the identification of minimum increases in the vital rates necessary to stabilize population growth or generate a growing population. From a demographic perspective of the AHA (Vélez-Espino and Koops 2007), the definition of recovery efforts is really the inverse of the allowable harm question.

In this paper we apply perturbation analysis of a stage-structured matrix population model portraying the life cycle of landlocked Atlantic salmon. Our specific goals are (i) to estimate maximum allowable harm on individual vital rates, (ii) to estimate minimum recovery efforts for individual vital rates, and (iii) to determine the relationship between allowable fishing mortality and catch size limits in sport fisheries of landlocked Atlantic salmon.

METHODS

Life history data on LOAS is virtually non-existent, and related information for landlocked North American Atlantic salmon populations is meagre. Our search of the relevant literature revealed one comprehensive published source for North American landlocked Atlantic salmon populations with sufficient life history data to apply a quantitative assessment of allowable harm based on the methodology of Vélez-Espino and Koops (2007). Thus, we collated all the relevant life history data from landlocked Atlantic salmon populations in Maine compiled by Warner and Havey (1985), consisting mainly of data for the duration of lotic life, age at maturity, spawning periodicity, age composition of spawning runs, sex ratio, proportion of individuals smolting as yearlings, proportion of individuals smolting at age 1+ and 2+, age-specific survival, partial information on length at age and the relationship between length and weight, and number of eggs per weight unit. Based on this description of landlocked Atlantic salmon life history, we modelled a stage-structured life cycle with seven stages (Figure 1), the first six stages corresponding to single ages. Stage 1 covered the period from spawning to the end of the first year of life (young-of-the-year; YOY). The last stage (stage 7) included all adult individuals from age 6+ to the maximum reproductive age (age 10+). Two alternative life histories are represented by the modelled life cycle: smolting at age 1+ and reproducing for the first time at age 2+, and smolting at age 2+ and reproducing for the first time at age 3+.

Information on age composition of spawning runs across tributaries and years was used to estimate the mean proportion of spawners at age (p_{age}; Figure 2). In addition, mean age at maturity (α) was computed as:

$$(1) \qquad \alpha = \sum_{age=2+}^{10+} p_{age} b$$

where b is the midpoint of the age interval (e.g., b = 3.5 for 3+ adults). This produced a mean age at maturity of 4.8 years. The relationships between age and length for ages 3+ to 7+ provided in Warner and Havey (1985) were used to compute length at age for younger and older fish (Figure 3). Power regressions were fit to minimum, mean, and maximum values of length at age. Similarly, data provided for Maine populations of landlocked Atlantic salmon were used to generate a relationship between length and weight (Figure 4) that combined with measures of relative fecundity (1.29 eggs/g) was used to fit a power regression representing the relationship between age and fecundity

(Figure 5). Finally, we incorporated minimum, mean, and maximum values of length at age into a single relationship between length and fecundity (Figure 6). These relationships were used to complete an Atlantic salmon life table and fecundity table including the number of eggs at age (m_{age}). Fertility (*f*; Figure 1c) of stage 7 was computed using the added proportions of spawners at age (p_{age}) and the average number of eggs (m_{age}) of fish spawning at ages 6+ and older.

For a thorough description of the approach to assess allowable harm (Figure 7) refer to Vélez-Espino and Koops (2007). Briefly, establishing equilibrium as the minimum acceptable population growth rate (i.e., $\lambda = 1$) allowable harm (τ_υ) is estimated as:

2) $$\tau_\upsilon \leq \left(\frac{1}{\varepsilon_\upsilon}\right)\left[\frac{1 - \Lambda}{\Lambda}\right]$$

where ε_υ is the elasticity (a measure of the sensitivity of population growth rate) of vital rate υ and Λ represents the geometric mean population growth rate of (i) the population growth rate determined by COSEWIC's criterion "A" for the status assessment of species based on observed or inferred rates of population decline ($\lambda_{\text{designation}}$), (ii) the maximum population growth at low densities determined from the Randall and Minns (2000) allometry between production per unit biomass (P/B) and weight at maturity for freshwater fishes (λ_{max}), and (iii) equilibrium ($\lambda = 1$) as an important dynamic attractor (Turchin 1995).

For projection matrices (e.g. Figure 1b), the influence of vital rates on population growth rate is indicated by the partial derivatives of λ with respect to m_{ij}, the individual elements of the matrix. Elasticities (ε_{ij}) scale these derivatives to adjust for different magnitudes of the vital rates (i.e., reproductive rates can be several orders of magnitude larger than survival probabilities), and they are calculated as:

3) $$\varepsilon_{ij} = \frac{\delta \log \lambda}{\delta \log m_{ij}}$$

Elasticities of matrix elements are additive and sum to unity. Multiplying the set of elasticities by λ produces a set of contributions which sum to λ, and the ε_{ij} themselves give the relative contribution of each transition to λ (de Kroon et al. 1986).

Equation 3 estimates the elasticities of matrix elements, not vital rates, which usually contribute to more than one matrix element. Thus, the chain rule for differentiation is used to compute vital rate elasticities:

4) $$\varepsilon_\upsilon = \frac{\upsilon}{\lambda}\frac{\delta\lambda}{\delta\upsilon} = \frac{\upsilon}{\lambda}\sum\frac{\delta\lambda}{\delta m_{ij}}\frac{\delta m_{ij}}{\delta\upsilon}$$

where υ is a lower-level variable (e.g., vital rates). Lower-level elasticities do not generally sum to 1, but they still indicate the relative sensitivity of λ to changes in life history traits and vital rates.

Inequality 2 estimates allowable harm for one vital rate at a time. Allowable harm for multiple perturbations will be therefore:

5) $$\sum_{\upsilon=1}^{k} \varepsilon_{\upsilon} \delta_{\upsilon} \leq 1 - \frac{1}{\Lambda}$$

where δ_{υ} is the proportional reduction in vital rate υ and k is the number of vital rates affected. Notice that inequalities 2 and 5 generate negative allowable harm values, where values closer to zero indicate less population resilience against harm in particular vital rates.

Regarding $\lambda_{designation}$, under COSEWIC criterion A a species is listed as endangered if $\lambda = 0.3^{1/10}$ or $\lambda = 0.3^{1/3\zeta}$ (whichever is longer), and as threatened if $\lambda = 0.5^{1/10}$ or $\lambda = 0.5^{1/3\zeta}$ (whichever is longer), where ζ is the generation time. The "extirpated" status for LOAS does not have a similar index of population decline. To address this methodological obstacle, we solved for the population growth rate generated by the mean transition matrix **A**. Matrix elements of **A** were computed with mean values of lower-level parameters (see best values of original estimates in Table 1):

$$\mathbf{A} = \begin{bmatrix} 0 & 0.4 & 16.7 & 24.7 & 34.1 & 38.5 & 28.9 \\ 0.054 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0.13 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0.027 & 0.595 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0.382 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0.48 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0.48 & 0.36 \end{bmatrix}$$

Matrix **A** generated a population growth rate of $\lambda_A = 0.81$, indicating an annual decrease of 19% in population size. Using λ_A instead of $\lambda_{designation}$, and using minimum (255 g), mean (601 g), and maximum (2166 g) weight at mean age at maturity (α) produced the geometric mean population growth rates 1.058, 1.024, and 0.99, respectively. Using a precautionary approach, which is part of the methodology described by Vélez-Espino and Koops (2007), when the smallest of these values is less than 1, harm is not allowed and recovery strategies should be implemented in the short term. However, given the status of LOAS, the fact that fish are been stocked continuously, and the great demand for an Atlantic salmon sport fishery, we used the intermediate value of Λ (1.024) to conduct an AHA that can guide regulations related to catch size limit and allowable fishing mortality. In addition, we determined minimum recovery efforts based on the smallest value of Λ (0.99). Knowledge about the maximum size-dependent allowable fishing mortality and the minimum increase in magnitude of significant vital rates necessary to stabilize population dynamics is intended to identify the life stages where recovery efforts should focus on improving population performance and guide management decisions. Extending the formulation for allowable harm to the determination of recovery efforts (ψ_{υ}) has the form

6) $$\psi_{\upsilon} \geq \left(\frac{1}{\varepsilon_{\upsilon}}\right)\left[\frac{1 - \Lambda}{\Lambda}\right]$$

Therefore, maximum allowable harm and minimum recovery efforts are $\tau_{\upsilon, max} = (1/\varepsilon_{\upsilon})(-0.024 / 1.024)$ and $\psi_{\upsilon, min} = (1/\varepsilon_{\upsilon})(0.01 / 0.99)$, respectively.

Before computing elasticities (ε_v) at least one matrix element must be adjusted to reflect the baseline geometric mean values (Λ) for which perturbation analyses are been conducted (Vélez-Espino and Koops 2007). It is recommended that the element(s) with the greatest uncertainty or those identified as potentially misleading be adjusted. From the vital rate values obtained from Warner and Havey (1985), the survival probabilities of 3+ adults and older fish included some local estimates incorporating both natural and fishing mortality. Therefore, we adjusted (increased) these values solving separately for $\Lambda = 1.024$ and $\Lambda = 0.99$.

Maximum allowable harm and minimum recovery efforts were computed separately from elasticities using a deterministic approach that uses only mean values of lower-level parameters (best values in Table 1) and a stochastic approach that uses the observed variation in lower level parameters (see Table 1). For the stochastic approach, we generated 1000 random matrices where vital rate values were drawn from uniform distributions defined by the limits for each vital rate in Table 1. Population growth rate (λ) was calculated for each matrix, elasticities of survival and fertility rates were calculated for each matrix, and a parametric bootstrap was used to estimate 95% confidence intervals for each elasticity value. In addition, following Vélez-Espino and Koops (2007), we assessed the effects of large human-induced reductions in vital rates by directly perturbing the projection matrices, thus relaxing the requirement for small changes in the application of inequalities 2 and 5 when non-linearity is exhibited between vital rates and population growth (see Mills et al. 1999, de Kroon et al. 2000).

This approach (Vélez-Espino and Koops 2007) also accounts for the inertial effect of population structure on future population size through the computation of population momentum (M). M was computed using Keyfitz's (1971) formulation:

7) $$M = \left(e'\left(v_1 w_0\right) w_1\right) \big/ \left(e' w_0\right)$$

where e' is a transposed vector of ones, w_0 is the dominant right eigenvector of the original projection matrix (before harm is allowed or before recovery strategy starts), and v_1 and w_1 are the dominant left and right eigenvectors of the new matrix (representing a population at equilibrium) produced by instantaneous changes in the vital rates (after harm or after recovery actions). The right eigenvector w represents the stable stage distribution, which indicates the proportion of the population in stage *i* once sufficient time has passed for fluctuations due to initial conditions to have finished, and the left eigenvector describes the reproductive value of an individual in stage *i* (de Kroon et al. 1986). Measures of M are centered on 1. If M > 1 the population will grow to a larger ultimate size following a perturbation and before stabilizing, and M < 1 indicate that the population will decline to a smaller ultimate size (Koons et al. 2006). Additional information on the population dynamics generated from estimates of population momentum is used to adjust maximum allowable harm or minimum recovery efforts when M < 1 by means of reducing $\tau_{\upsilon,max}$ or increasing $\psi_{\upsilon,min}$ until population momentum is at least 1. The most direct way of adjusting $\tau_{\upsilon,max}$ or $\psi_{\upsilon,min}$ is through direct perturbation of the transition matrix, regressing M on $\tau_{\upsilon,max}$ or $\psi_{\upsilon,min}$ and computing $\tau_{\upsilon,max}$ or $\psi_{\upsilon,min}$ for M = 1.

Finally, simultaneous perturbations on more than one vital rate were used to compute maximum allowable fishing mortality per composite vital rate ($\omega_{\upsilon,max}$) from deterministic and stochastic approaches, and maximizing the value of inequality 5. Composite vital rates used to compute $\omega_{\upsilon,max}$ were $\sigma_6+\sigma_7$, $\sigma_5+\sigma_6+\sigma_7$, and $\sigma_4+\sigma_5+\sigma_6+\sigma_7$, where subscripts represent stages. The relationships between $\omega_{\upsilon,max}$ and minimum, mean, and maximum length at age were used to describe the relationship between catch size limit and allowable fishing mortality. For stage 7 (6+ adult and older) we used only size information from age-6+ individuals. All computations of population growth rates, elasticities, direct perturbations, population momentum, and simulations were conducted with the aid of MATLAB version 7 (The Mathworks, Inc., Natick, Massachusetts).

Results for maximum allowable harm values for vital rates were summarized in a comprehensive table as suggested by Vélez-Espino and Koops (2007). In this table, deterministic results from analytical solutions (elasticities) and direct perturbations of projection matrices are contrasted against mean and lower bounds of 95% confidence intervals from the stochastic approach. Mean values from the stochastic approach should be compared with the deterministic values, and the lower bounds of the confidence intervals are presented to guide risk-averse decisions, although this output may not always provide the most conservative values. Following a precautionary approach, Vélez-Espino and Koops (2007) recommend using the lowest value of maximum allowable harm among the four outputs: deterministic elasticities, deterministic direct perturbations, stochastic mean, and stochastic lower bound. Population momentum is also part of the summary table, and maximum allowable harm is kept unaltered if and only if $M \geq 1$. We use similar tables to summarize the results for minimum recovery efforts and maximum allowable fishing mortality. Logically, in the summary table for minimum recovery efforts, the stochastic upper bound replaced the lower bound and recommendations are based on the highest value among the four outputs presented.

Incorporating available data for LOAS

Partial information on biological characteristics of LOAS was obtained from an Atlantic salmon stocking survey conducted on the Credit River for years 1990 and 1991 and angler surveys for years 1988 to 1994 (pers. comm., J. Bowlby, OMNR). Information from the Credit River allowed us to generate length-weight and length at age relationships; information from the angler surveys allowed us to generate a length-weight relationship. These relationships were used to (i) compare the LOAS length-weight relationships with that generated for the Maine populations, (ii) compare the LOAS length at age relationship with those generated for Maine populations, and (iii) analyze the effect of life history differences on our estimates of maximum allowable fishing mortality as a function of catch size limit.

RESULTS

Similar elasticity patterns were found for $\Lambda = 1.024$ and $\Lambda = 0.99$ (Figure 8). Deterministically, population growth rates of Atlantic salmon were more sensitive to changes in the survival of stage 2 (1+ smolt) followed by stages 1 (YOY) and 3 (2+ smolt-adult), both with slightly lower elasticities. Survival of stages 6 (5+ adult) and 7 (6+ and older) had the lowest survival elasticities, similar in magnitude to fertility elasticities of stages 5 (4+ adult) and 7 (6+ and older). The vital rates with the lowest deterministic elasticities were fertility for stages 3 (2+ smolt-adult) and 4 (3+ adult). Mean elasticities obtained from the stochastic approach were consistent with the deterministic pattern. However, wide 95% confidence intervals made elasticity rankings for individual vital rates elusive. Nevertheless, population growth rates were seemingly most sensitive to proportional changes in the survival of stages 1, 2, and 3. Among the fertility rates the fertility of stage 5 (4+ adult) had the potentially highest relative importance.

Similar values of maximum allowable harm (Table 2) were obtained from the four outputs for survival of the first four stages (YOY to 3+ adult) and maximum allowable harm was practically identical for the first three stages. Large differences among outputs were produced for maximum allowable harm for survival rates of stages 5, 6 and 7 and fertility rates of all reproductive stages. Any value of allowable harm greater than 1 for a given vital rate suggests that population growth would not reach equilibrium even after completely cancelling that vital rate for one generation. The stochastic lower bound produced the lowest allowable harm in most cases, excepting for the survival of 5+ and 6+ and older adults and the fertility of 6+ adults; direct perturbations of projection matrices generated the lowest values for those vital rates. Based on the precautionary approach, an allowable harm greater than a 7% reduction in the survival of YOY, 1+ smolt, or 2+ smolt-adult, 10% reduction in the survival of 3+ adult, 16% reduction in the survival of 4+ adult, 25.5% reduction in the survival of 5+ adult, 25.2% reduction in the survival of 6+ and older, 21% reduction in the fertility rate of 2+ smolt-adult, 15% reduction in the fertility rate of 3+ adult, 11% reduction in the fertility of 4+ adult, 22% reduction in the fertility rate of 5+ adult, or 25% reduction in the fertility rate of 6+ and older adults is expected to jeopardize the survival and future recovery of the population.

Minimum recovery efforts (Table 3) paralleled those for maximum allowable harm. Similar values were produced by the different outputs for the survival of the first four stages with larger discrepancies in the survival values of stages 5, 6 and 7, and the fertility rates of all reproductive stages. The stochastic upper bound produced the highest recovery efforts in most cases, except for the survival of the first three stages, where direct perturbations of projection matrices generated the highest values. The most effective way of increasing population growth rate is through increases in the survival of YOY, 1+ smolt, and 2+ smolt-adult, followed by increases in the survival of 3+ and 4+ adults (Table 3). Under a risk-averse perspective, the proportional increase in vital rate values necessary to stabilize a potentially declining population should be 5.5% in the survival of YOY, 1+ smolt, or 2+ smolt-adult, 11% in the survival of 3+ adults, 55% in the survival of 4+ adults, and extremely large for the survival of 5+ and 6+ and older fish and for the fertility of most reproductive stages. Extremely large values for minimum recovery efforts of these vital rates (most of them biologically unachievable) simply reflect the impossibility of significantly improving population performance through substantial increments in the magnitude of these vital rates. Nevertheless, doubling the reproductive success of 4+ adults is expected to stabilize population dynamics. Even larger increases would be necessary for other reproductive stages.

Maximum allowable harm for composite vital rates (particularly survival of adult stages) was computed after incorporating into a single composite stage more than one life stage. The effect of perturbations on a composite vital rate was computed by adding the elasticities of individual vital rates or through simultaneous and identical direct perturbations of lower-level parameters in the transition matrix. Fishing mortality affecting stages 6 and 7 reduced the maximum allowable harm from 25.2% (maximum allowable harm for survival of stage 7 alone) to 14%. Fishing stages 5, 6, and 7 further reduced maximum allowable harm to 8%. The inclusion of stage 4 reduced maximum allowable harm even further down to 4% (Table 4). When these results are related to length at age, maximum allowable fishing mortality increases exponentially with increases in catch size limit (Figure 9). Variation in length at age is reflected in the rather large variation in maximum allowable fishing mortality for a given size limit. For example, with a 40 cm size limit maximum allowable harm is less than 1% for the curve representing maximum length at age, 8% for the mean curve, and about 25% for the curve representing minimum length at age. Based on the mean curve, a fishing mortality of 100% in fish larger than 61 cm could be allowed without compromising population stability. Nevertheless, following a precautionary approach, regulations should be based on maximum length at age, indicating that fishing mortality should be less than 28% for the current 63 cm size limit.

Inferences from LOAS biological characteristics

The relationship between length and weight for Lake Ontario Atlantic salmon was well represented, even for large individuals, by the regression curve generated from Maine populations (Figure 10). This match suggests similar condition factors for landlocked Atlantic salmon in Lake Ontario and Maine. However, greater growth is apparent in Lake Ontario populations where an average age-2 individual can be 13 cm larger than a large age-2 Maine fish. This difference can be as big as 17 cm for age-10 individuals (Figure 11). However, there is a relatively poor fit ($R^2 = 0.26$) to the growth data for Lake Ontario, probably due to the small sample size ($n = 28$), suggesting that caution should be taken when interpreting growth differences between Maine and Lake Ontario Atlantic salmon populations.

As a result of greater somatic growth in Lake Ontario, allowable fishing mortality for the current catch size limit (63 cm) was reduced from 28% (the value obtained using Maine data) to 2% (Figure 12). The main biological reason for this reduction in allowable fishing mortality is that a 63 cm fish will be three years old at the time of capture with a low probability of having reproduced even once. Alternatively, to increase allowable fishing mortality the catch size limit would have to be substantially increased. For example, to keep an allowable fishing mortality of 28%, as was computed from the Maine data, the catch size limit would have to be increased to 80 cm. At this size an average fish would be 7 years old, matching the minimum age at capture (7-10 years old) for Maine populations.

DISCUSSION

Three main conclusions emerge from our analyses. First, the existence of fishing mortality on LOAS and management efforts to improve population performance can coexist by implementing effective fishing regulations and recovery strategies. Second, the most effective and feasible way to improve population fitness is through the survival rates of the lotic, juvenile life stages YOY, 1+ smolt, and 2+ smolt-adult. Third, catch size limits can be used as a conservative, risk-averse regulation for maximum allowable fishing mortality.

Coexistence of recreational fishery and recovery efforts

Our first conclusion that recovery strategies can be implemented while allowing some level of fishing mortality is supported by the low sensitivity of population performance to moderate mortality exerted upon older fish. More specifically, if the population growth rate was highly sensitive to a reduction in the survival of large individuals (desirable catch) then the coexistence of effective recovery strategies and allowable fishing mortality would not be possible. The implementation of a year-round closure of fishing in tributaries of Lake

Ontario is consistent with our results. Improving survival of pre-maturing individuals in streams is expected to be the most effective way of improving population performance. This capacity of our model to guide management efforts through the identification of vital rates with the greatest contributions to population growth rates can be used to identify both the points in the life cycle most sensitive to harm and those with the greatest potential to effectively improve population fitness.

Recovery feasibility

Our second conclusion is that increasing the survival of immature individuals in streams is the most feasible way to increase LOAS population growth rates with relatively low effort. Increasing survival rates by 6% in any of the three lotic stages is expected to produce equilibrium, and any improvement beyond this 6% is expected to produce positive population growth rates. Given that allowable harm can be relatively large for the fertility of age-2+ fish, management efforts should focus on the smolt portion of age-2+ fish. Suppressing the reproduction of age-2+ individuals is expected to have a minor impact on population performance, but high mortality of age-2+ immature individuals is expected to have a relatively large influence on population growth rates. Thus, along with the prohibition of fishing activities in Lake Ontario tributaries, habitat rehabilitation targeting spawning grounds and juvenile habitat are recommended to increase survival rates of YOY, 1+, and 2+ fish. Habitat rehabilitation strategies could include vegetation buffer strips to reduce the impact of non-point source pollution, in-stream habitat structures to enhance stream energy and increase velocities, gravel cleaning to reduce silt content, aeration and oxygenation techniques, rehabilitation of water flows required by juveniles (including the protection of flow ranges), replenishment of spawning gravels, and channel modifications to improve in-stream habitat, among many others (Hendry et al. 2003).

As a corollary from our second conclusion, attempting to improve fertility rates is not recommended for two reasons: relatively low sensitivity of population growth rates to fertility improvements and the difficulty of implementing management actions improving one or more of the life history elements involved in fertility rates such as number of eggs, age composition of spawning runs, spawning periodicity, or sex ratio. Manipulating sex ratios to maximize effective population size would be an option but is not considered here because our models use a balance sex ratio, which is characteristic of an ideal sexual population.

Allowable fishing mortality

The current fishing size limit of 63 cm (COSEWIC 2006) is conservative if somatic growth of LOAS is appropriately represented by data for landlocked Maine population, based on the majority of 63 cm fish being 7 to10 years old and will have already reproduced at least once. Nevertheless, it would be necessary to incorporate in the regulation a maximum fishing mortality through control upon the annual number of permits, considering the concession of keeping only one fish per day. Further, as a result of the steepness of the response curves, allowable fishing mortality is highly sensitive to small reductions in the catch size limit. For instance, reducing the size limit from 63 cm to 60 cm reduces allowable fishing mortality from 28% to 17%. This feature of the response curves may become particularly important when misidentification occurs with other salmonid species for which size limits are lower. Depending on levels of misidentification, by-catch mortality has the potential to significantly change the allowable fishing mortality for Atlantic salmon.

In addition, hook mortality must be considered. Depending on the kind of lure and hook used, mortality from hooking injuries on Maine landlocked populations of Atlantic salmon was as high as 90% (Warner and Havey 1985).

Incorporating biological characteristics of LOAS indicate that greater somatic growth in Lake Ontario would reduce maximum allowable fishing mortality or require a substantial increase in the catch size limit. However, two factors prompt caution interpreting these results: (1) the uncertainty associated with age estimates in the data sources and (2) the lack of independence of life history traits and demographic rates within a population. The paucity of data available for LOAS and the uncertainty associated with the available data precluded construction of a population model specifically representative of Lake Ontario populations. It is possible that uncertainty around the time stocked individuals spend in the lake may cause underestimation of age in sampled fish. Hence, the LOAS growth pattern depicted by our power regression should be considered representative of maximum growth rates for Lake Ontario. Differing growth patterns in Lake Ontario will not affect our projections of population response to perturbation on survival as our models are basically age-structured. Consequently, the sensitivity of population growth rates to stage-specific fishing mortality are not influenced either. It is the relationship between catch size limit and maximum allowable fishing mortality that changes with variation in growth patterns. Fecundity estimates will change with growth patterns because fecundity increases with length, and increasing stage-specific fertility is expected to reduce the sensitivity of population growth rate to perturbations on fertility. We do not further explore the influence of growth patterns on fertility elasticities because it is considered irrelevant to the analysis of allowable fishing mortality.

About the methodology

Considered as a pressing need (DFO 2004, DFO 2005c), a quantitative, scientifically robust approach to assessing allowable harm and identifying recovery efforts that is applicable to data poor populations and is flexible enough to accommodate the life histories observed in aquatic species has remained a challenge. Our approach represents an effort in that direction but also introduces a first attempt to unify the three essential elements of a recovery potential assessment (allowable harm, critical habitat, and recovery targets; DFO 2005a, 2005b) within a modelling framework. Our approach also integrates scientific advice on allowable harm and components of recovery plans, which has been identified as crucial to increasing the likelihood of achieving recovery targets within reasonable timeframes (DFO 2004). The unifying factor in our approach is the use of population growth rates as the main ecological currency to evaluate both allowable harm and recovery efforts. This provides the advantage of defining recovery efforts as dynamic parameters instead of static, probably elusive, estimates of historic population size or range. Ultimately, increasing population size and/or range are a consequence of positive population growth rate. The ecological basis of our modelling approach not only facilitates the integration of results but also provides a common working framework to enhance the effectiveness of management decisions within SARA and the communication of goals, strategies, and results.

Although the present application to LOAS did not exploit the model compartment referred as “habitat-based bridge modelling” (Figure 7), it is important to mention that when habitat-based information is available, maximum allowable harm can be estimated in terms of habitat quantity or quality. Availability of information on habitat supply and demand allowed Vélez-Espino and Koops (2007) to assess maximum allowable habitat loss in a Canadian population of black redhorse (*Moxostoma duquesnei*). The effect of habitat loss on population growth rates, as implemented in black redhorse, represented only the impact of changes in habitat quantity on population dynamics through effects on survival rates as a result of density-dependent mortality. However, limitations in habitat quantity can also affect somatic growth rates (e.g., Van Winkle et al. 1993) or increase the propensity to emigrate (e.g., Grant and Kramer 1990). Further, the impact of changes in habitat quality, which can be as important as habitat quantity, can be readily incorporated into the model once the relationship between some habitat component (biotic or abiotic) and affected vital rate has been empirically determined (e.g., Hayes et al. 1996, Eby et al. 2005).

Compensatory mechanisms increasing survival rates of specific stages as a result of reducing densities in other stages were not included in our models because (a) the incorporation of density dependence is not justified by the current status (extirpated) of LOAS, characterized by extremely low population size and spawning returns, (b) density-independent variation in survival rates is in general more important than density dependence at low population size (e.g., Grant and Kramer 1990, Caley et al. 1996, Jones et al. 2003), and (c) stage-specific abundance time series necessary for this kind of analysis do not exist for LOAS. Nevertheless, matrix population models are suitable for explicit incorporation of density dependence (see Caswell 2001 and study cases therein), where particular functions can be used to project population responses in the presence of compensatory mechanisms. Wide density-independent variation in the vital rates was included in the stochastic approach, where the underlying assumption is not that density dependence is absent but that the effect of density on population growth rate does not change over the range of population densities in the present and likely to occur in the short future. Lastly, compensatory mechanisms would increase population resilience to harm as a result of increased survival rates with decreased densities. Following a precautionary approach, the absence of density dependence produces more risk-averse scenarios than those assuming compensation in spite of currently low densities.

The most important limitation of our analysis comes from the use of life history data from landlocked Atlantic salmon populations in Maine to parameterize the models. The use of life history data from closer taxonomic relatives or geographically close populations has been a common practice in conservation biology (Caughley and Gunn 1996, Morris and Doak 2002), justified by the similarity of life history patterns and the need for quantitative approaches guiding decisions with more scientific basis than trial and error decisions or expert opinion. Using data exclusively from Maine landlocked populations was considered important because building models with life history data from a single population or a discrete number of highly related subpopulations preserves correlations and covariance among life history traits. In general, variation in demographic rates is not independent and is likely to be correlated. Thus, the incorporation of partial life history data requires caution because temporal correlation and covariance can strongly influence the values of elasticities (Saether and Bakke 2000). Correlations among life history traits can have important impacts on population growth rate (Caswell 2001) and is likely to alter the width of confidence intervals for population responses (see Doak et al. 1994).

Uncertainty around the actual vital rate values for landlocked populations of Atlantic salmon in Lake Ontario has been partly offset by the implementation of a stochastic approach where large random variation in the value of individual vital rates has been simulated. However, important differences in age at first maturity and the age composition of spawning runs between Maine and Lake Ontario landlocked populations may significantly change population responses to fishing mortality; although the ranking of relative importance of vital rates will probably be preserved considering that our models also incorporated important variation in the age composition of spawning runs. The paucity of available information precluded a complete and robust analysis of these population attributes in LOAS. Based on a sample size of 28 individuals (16 females and 12 males) in the Credit River, spawning runs consisted of 11% 1+, 71% 2+, and 18% 3+ fish. Our stage-structured model considered an age at first maturity of 2+ and therefore did not include an alternative life history with 1+ spawners. However, the Credit River data indicates that only a small portion of the spawning run is represented by 1+ fish. The synthesis of large-scale life history variation and growth patterns in Atlantic salmon by Hutchings and Jones (1998) shows that throughout its entire range Atlantic salmon smolting age has not been reported to occur at age 0+, which would be the case for an age 1+ spawner (usually Atlantic salmon do not mature the year they smolt; Jonsson and Jonsson 1993); smolting can take place at ages ranging from 1+ to 5+. This observed variation in smolting age and the uncertainty associated with age estimates in our data source suggest that more data will be necessary before properly and confidently incorporating this potential life cycle path into the model as well as a local metric of mean age at maturity that might change the value of geometric mean population growth rates (Λ).

As new data on LOAS become available it can be readily incorporated into the models. Life history theory predicts that earlier age at maturity is an adaptive response to increased somatic growth rate (Roff 1992, Stearns 1992, Hutchings 1993) and this prediction has been corroborated for Atlantic salmon (Hutchings and Jones 1998). Smolt age in Atlantic salmon is negatively associated with length of the growing season (Power 1981), and this negative association persists throughout its geographic range (Metcalfe and Thorpe 1990). Hence, one way of refining our estimates of smolting age could be through the temperature- and photoperiod-based metric of somatic growth rate in streams developed by Metcalfe and Thorpe (1990), which accounts for 82% of the variation in smolt age. This adjustment is expected to have larger effects on LOAS population dynamics and population responses than proportional changes in vital rates (see Lewontin 1965, Heppell et al. 2000). Moreover, bottlenecks in one or more LOAS life stages can have important impacts on population performance and therefore their identification and quantification is essential for a more realistic assessment of allowable harm and recovery efforts. From our analyses, it appears that reproductive bottlenecks will have a smaller effect in LOAS inability to develop self-sustaining populations relative to bottlenecks affecting early survival. Similarly, a bottleneck affecting survival of old adults inhabiting the lake would have a low negative impact on population performance relative to the survival of stream dwelling juveniles.

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Table 1. Low, best, and high values of lower-level parameters annual survival (σ), transition probabilities (γ), proportion of spawning fish (*p*), spawning periodicity (*q*), number of eggs (*m*), fertility (*f*; see text), proportion of fish smolting at age 1+ (z_{G2}), and proportion of fish smolting at age 2+ (z_{H2}) for the seven stages of the modelled Atlantic salmon life cycle. Original estimates of survival rates for 3+, 4+ and older fish were 0.20 (low), 0.38 (best) and 0.56 (high), and 0.42 (low), 0.48 (best), and 0.54 (high), respectively. These values were adjusted to solve for geometric means of $\Lambda = 1.024$ and $\Lambda = 0.99$ (see text). Numbers in parentheses represent adjusted adult survival rates corresponding to the declining population scenario.

		Trait							
Stage	**Value**	σ	γ	*p*	*q*	*m*	*f*	z_{G2}	z_{H2}
YOY	low	0.007	1.000	-	-	-	-	-	-
YOY	best	0.054	1.000	-	-	-	-	-	-
YOY	high	0.099	1.000	-	-	-	-	-	-
1+ Smolt	low	0.190	1.000	-	-	-	-	0.190	-
1+ Smolt	best	0.280	1.000	-	-	-	-	0.465	-
1+ Smolt	high	0.370	1.000	-	-	-	-	0.740	-
2+ Smolt, Adult	low	0.490	1.000	0.000	0.330	61	0.000	-	0.260
2+ Smolt, Adult	best	0.595	1.000	0.045	0.500	270	3.065	-	0.535
2+ Smolt, Adult	high	0.700	1.000	0.173	1.000	1311	113.402	-	0.810
3+ Adult	low	0.560	1.000	0.000	0.330	136	0.000	-	-
3+ Adult	best	0.769 (0.714)	1.000	0.242	0.500	465	28.133	-	-
3+ Adult	high	0.769 (0.714)	1.000	0.702	1.000	1620	568.620	-	-
4+ Adult	low	0.560	1.000	0.129	0.330	330	7.024	-	-
4+ Adult	best	0.769 (0.714)	1.000	0.312	0.500	776	60.528	-	-
4+ Adult	high	0.769 (0.714)	1.000	0.514	1.000	2798	719.086	-	-
5+ Adult	low	0.560	1.000	0.014	0.330	513	1.185	-	-
5+ Adult	best	0.769 (0.714)	1.000	0.259	0.500	1100	71.225	-	-
5+ Adult	high	0.769 (0.714)	1.000	0.517	1.000	3011	778.344	-	-
6+ and older	low	0.560	0.250	0.003	0.330	1656	0.820	-	-
6+ and older	best	0.769 (0.714)	0.250	0.142	0.500	2263	80.337	-	-
6+ and older	high	0.769 (0.714)	0.250	0.382	1.000	4433	846.703	-	-

Table 2. Summary of maximum allowable harm estimates per vital rate ($\tau_{\upsilon,\ max}$) from deterministic and stochastic approaches. At the bottom of the table are shown the population momentum values for each vital rate. Bold values indicate the maximum allowable harm recommended for management decisions.

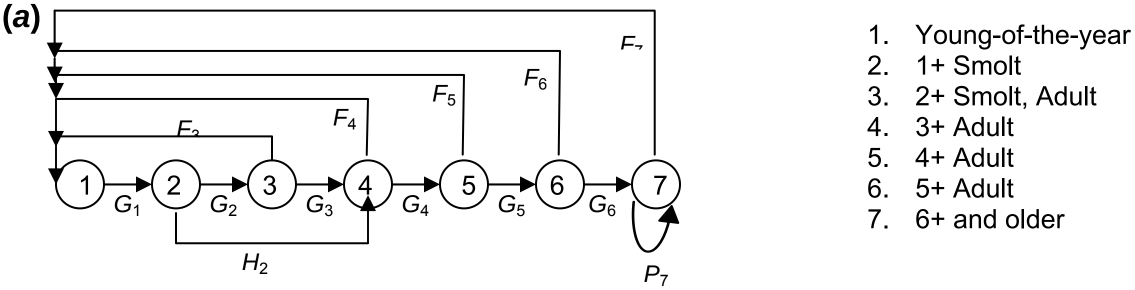
	$\tau_{v,\ max}$											
	σ_{YOY}	$\sigma_{1+\ smolt}$	$\sigma_{2+\ smolt,\ adult}$	$\sigma_{3+\ Adult}$	$\sigma_{4+\ Adult}$	$\sigma_{5+\ Adult}$	$\sigma_{6+\ and\ older}$	$f_{2+\ smolt,\ adult}$	$f_{3+\ Adult}$	$f_{4+\ Adult}$	$f_{5+\ Adult}$	$f_{6+\ and\ older}$
Deterministic (elasticities)	-0.11	-0.11	-0.11	-0.13	-0.19	-0.31	-0.29	-6.54	-1.33	-0.35	-0.49	-0.31
Deterministic (direct perturbation)	-0.11	-0.11	-0.11	-0.125	-0.17	**-0.255**	**-0.252**	-	-	-0.33	-0.55	**-0.25**
Stochastic (mean)	-0.08	-0.08	-0.09	-0.14	-0.32	-0.74	-1.34	-0.61	-0.36	-0.22	-0.55	-0.74
Stochastic (lower bound)	**-0.07**	**-0.07**	**-0.07**	**-0.1**	**-0.16**	-0.26	-0.37	**-0.21**	**-0.15**	**-0.11**	**-0.22**	-0.26
Population momentum	5.12	4.98	4.85	4.79	4.69	4.58	4.36	-	-	4.79	4.68	4.46

Table 3. Summary of minimum recovery efforts per vital rate ($\psi_{\upsilon,min}$) from deterministic and stochastic approaches. At the bottom of the table are shown the population momentum values for each vital rate. Bold values indicate the minimum recovery efforts recommended for management decisions.

	$\psi_{v,\ min}$											
	σ_{YOY}	$\sigma_{1+\ smolt}$	$\sigma_{2+\ smolt,\ adult}$	$\sigma_{3+\ Adult}$	$\sigma_{4+\ Adult}$	$\sigma_{5+\ Adult}$	$\sigma_{6+\ and\ older}$	$f_{2+\ smolt,\ adult}$	$f_{3+\ Adult}$	$f_{4+\ Adult}$	$f_{5+\ Adult}$	$f_{6+\ and\ older}$
Deterministic (elasticities)	0.05	0.04	0.05	0.05	0.08	0.14	0.14	2.53	0.51	0.14	0.2	0.14
Deterministic (direct perturbation)	**0.055**	**0.055**	**0.055**	0.064	0.091	0.15	0.14	2.4	0.42	0.21	0.25	0.15
Stochastic (mean)	0.04	0.03	0.04	0.06	0.14	0.34	0.63	0.25	0.15	0.1	0.24	0.34
Stochastic (upper bound)	0.05	0.04	0.05	**0.11**	**0.55**	**7.78**	**20.22**	**7.22**	**2.53**	**0.96**	**4.04**	**7.78**
Population momentum	4.55	4.6	4.64	4.69	4.74	4.79	4.97	4.6	4.65	4.69	4.74	4.86

Table 4. Summary of maximum allowable fishing mortality for the composite vital rate ($\omega_{\upsilon,max}$) from deterministic and stochastic approaches. At the bottom of the table are shown the population momentum values for each vital rate. Bold values indicate the maximum allowable fishing mortality recommended for management decisions.

	$\omega_{v,\ max}$		
	$\sigma_6 + \sigma_7$	$\sigma_5+\sigma_6+\sigma_7$	$\sigma_4+\sigma_5+\sigma_6+\sigma_7$
Deterministic (elasticities)	-0.15	**-0.08**	-0.05
Deterministic (direct perturbation)	**-0.14**	**-0.08**	-0.05
Stochastic (mean)	-0.48	-0.19	-0.08
Stochastic (lower bound)	-0.15	**-0.08**	**-0.04**
Population momentum	4.42	4.52	4.61



(b)

$$n_1(t+1) = F_3\,n_3(t) + F_4\,n_4(t) + F_5\,n_5(t) + F_6\,n_6(t) + F_7\,n_7(t)$$

$$n_2(t+1) = G_1\,n_1(t)$$

$$n_3(t+1) = G_2\,n_2(t)$$

$$n_4(t+1) = G_3\,n_3(\mathrm{t}) + H_2\,n_2(t)$$

$$n_5(t+1) = G_4\,n_4(t)$$

$$n_6(t+1) = G_5\,n_5(t)$$

$$n_7(t+1) = G_6\,n_6(t) + P_7\,n_7(t)$$

$$\mathbf{A} = \begin{pmatrix} 0 & F_2 & F_3 & F_4 & F_5 & F_6 & F_7 \\ G_1 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & G_2 & 0 & 0 & 0 & 0 & 0 \\ 0 & H_2 & G_3 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & G_4 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & G_5 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & G_6 & P_7 \end{pmatrix}$$

(c)

$$\left.\begin{array}{l} G_i = \sigma_i\ \gamma_i \\ H_2 = z_{H2}\,(\sigma_2\gamma_2)\,(\sigma_3\,\gamma_3) \\ G_2 = z_{G2}\,(\sigma_2\gamma_2) \\ P_i = \sigma_i\,(1-\gamma_i) \\ F_i = f_i\,P_i + f_{i+1}\,G_i \\ F_4 = f_5\,G_4 + f_5\,H_2 \\ f_i = m_\mathrm{i}\ p(\mathrm{i})\ q\ \varphi \\ \gamma_i = \mathrm{T}_\mathrm{i}^{-1} \end{array}\right\}$$

z_{G2} – Proportion of fish smolting at age 1+
z_{H2} – Proportion of fish smolting at age 2+
σ_i – Annual survival rate of stage *i*
γ_j - Probability of moving from *i* to *i*+1 given σ_i
m_i – Number of eggs at stage *i*
$p(i)$ – Proportion of fish spawning at stage *i*
φ - Proportion of eggs producing females
q – Inverse of spawning periodicity (yr^{-1})
f_i – Fertility: annual number of female offspring per adult female at stage *i*
T_i – Duration (in years) of stage *i*

Figure 1. (a) Generalized landlocked Atlantic salmon life cycle, (b) corresponding stage-structured projection matrix and related projection formulas, and (c) matrix element formulations. The life cycle is modelled as a post-breeding projection matrix, so fecundity coefficients (F_i) depend on adult survival through the previous year and the stage-specific fertility (f_j). Juveniles moving into the 2+ smolt-adult stage the following year will also contribute to reproductive output, thus the fecundity coefficient for stage 2 (F_2). The first six stages correspond to ages 0+ to 5+, respectively; stage 7 includes all age 6+ and older individuals. P_i the probability of surviving and remaining in the same stage, and G_i the probability of surviving and moving to the next stage. H_2 represents the probability that 2+ smolts survive between stages 2 and 4. n_i is the number of individuals in stage *i*; *t* is the projection time in years.

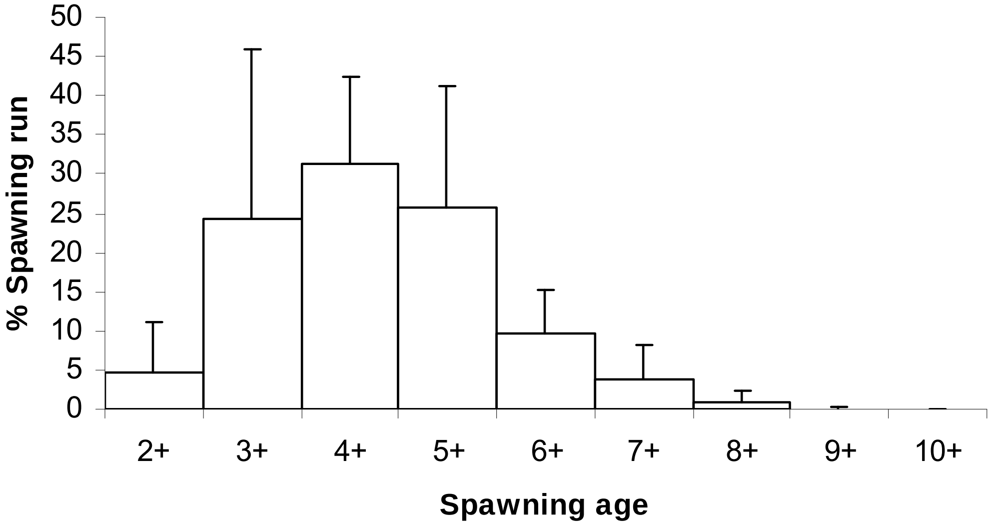


Figure 2. Age composition of landlocked Atlantic salmon spawning runs in Maine lakes. Values represent means across 13 tributaries during years 1951-1979. Error bars represent one standard deviation.

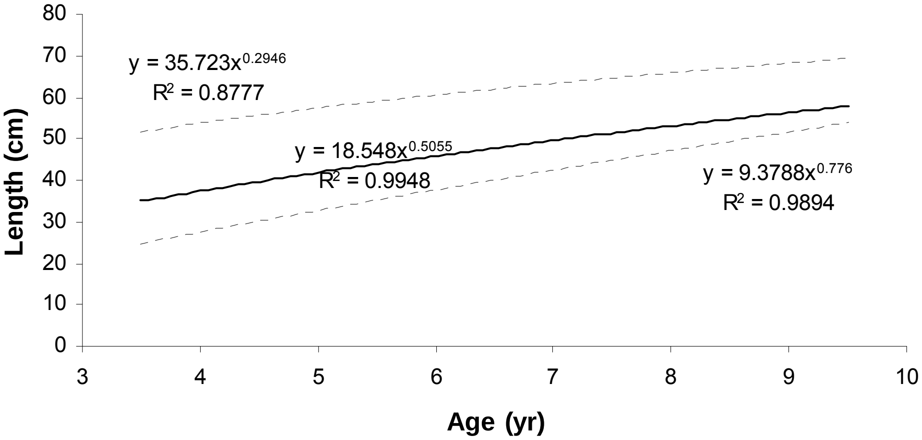


Figure 3. Growth of landlocked Atlantic salmon in Maine lakes. Growth patterns are depicted for minimum, mean, and maximum length at age. Power regressions were fit with annual mean values (1952-1981). Sample size per age is: 3+ (n = 40); 4+ (n = 43); 5+ (n = 41); 6+ (n = 33); 7+ (n = 21).

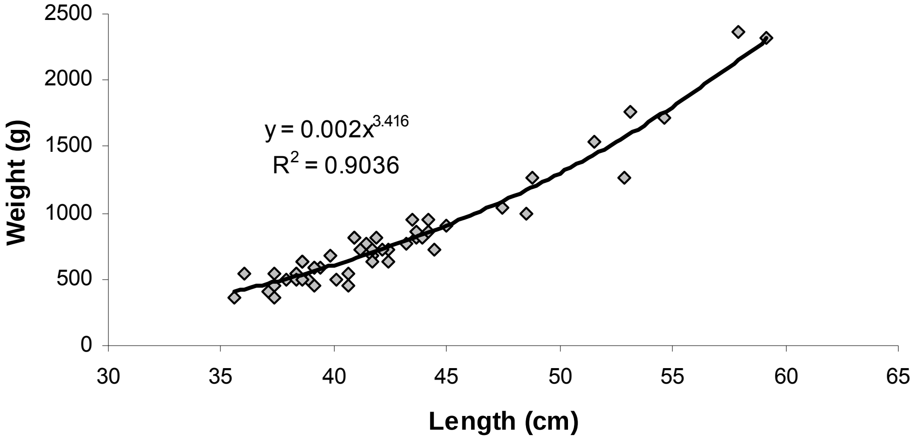


Figure 4. The relationship between mean total length and weight of landlocked Atlantic salmon in Maine spawning runs and sport fisheries (n = 52). Data collected from 1957 to 1981.

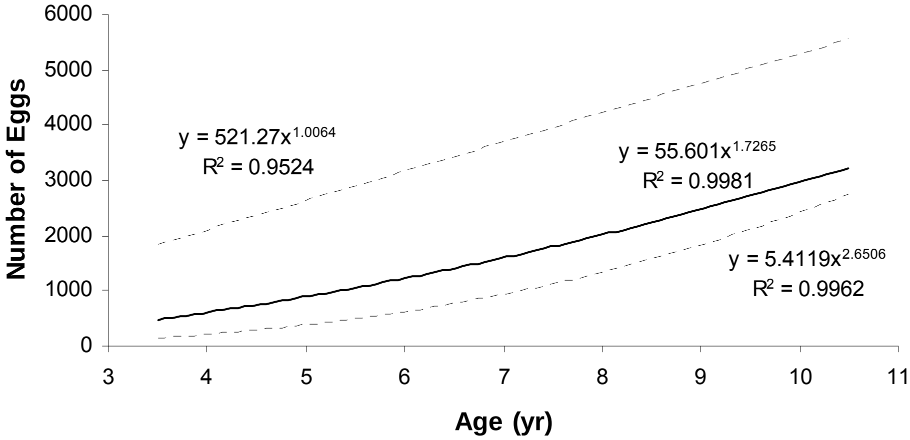


Figure 5. The relationship between age and number of eggs (*m*). Power regressions were fit to minimum, mean, and maximum age-specific egg number. The term *m* was computed as *y* 0.002L $^{3.416}$, where *y* is relative fecundity (1.29 eggs/g) and L is total body length (cm).

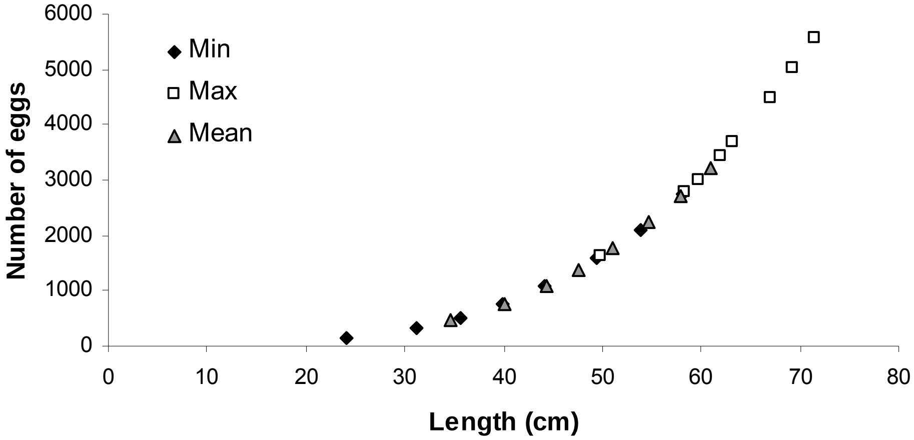


Figure 6. The relationship between total body length and number of eggs incorporating minimum, mean, and maximum length at age. This relationship fit by the power regression $m = 0.0026L^{3.416}$ (n = 24; $R^2 = 1$).

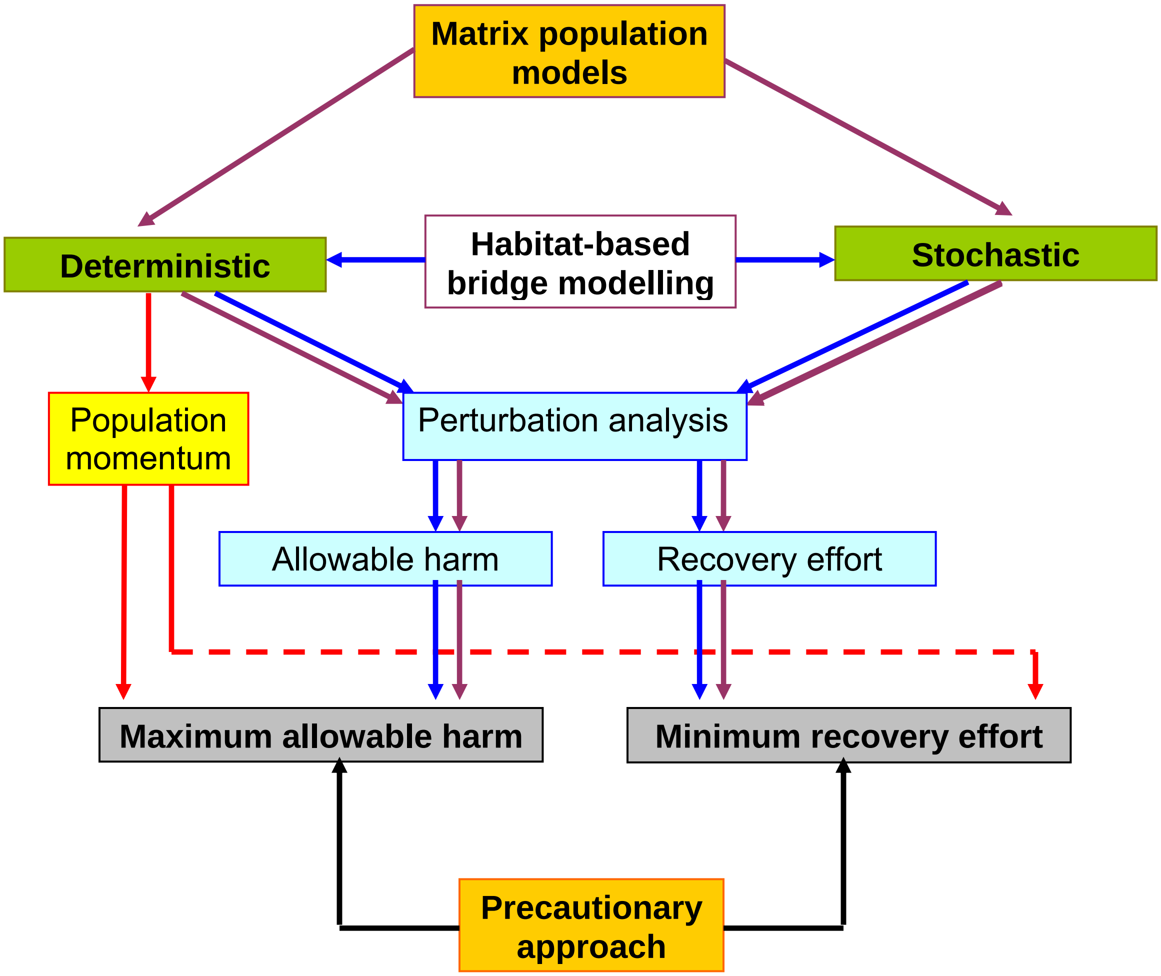


Figure 7. Schematic representation of the methodology applied to the quantitative assessment of allowable harm and recovery efforts (Vélez-Espino and Koops 2007).

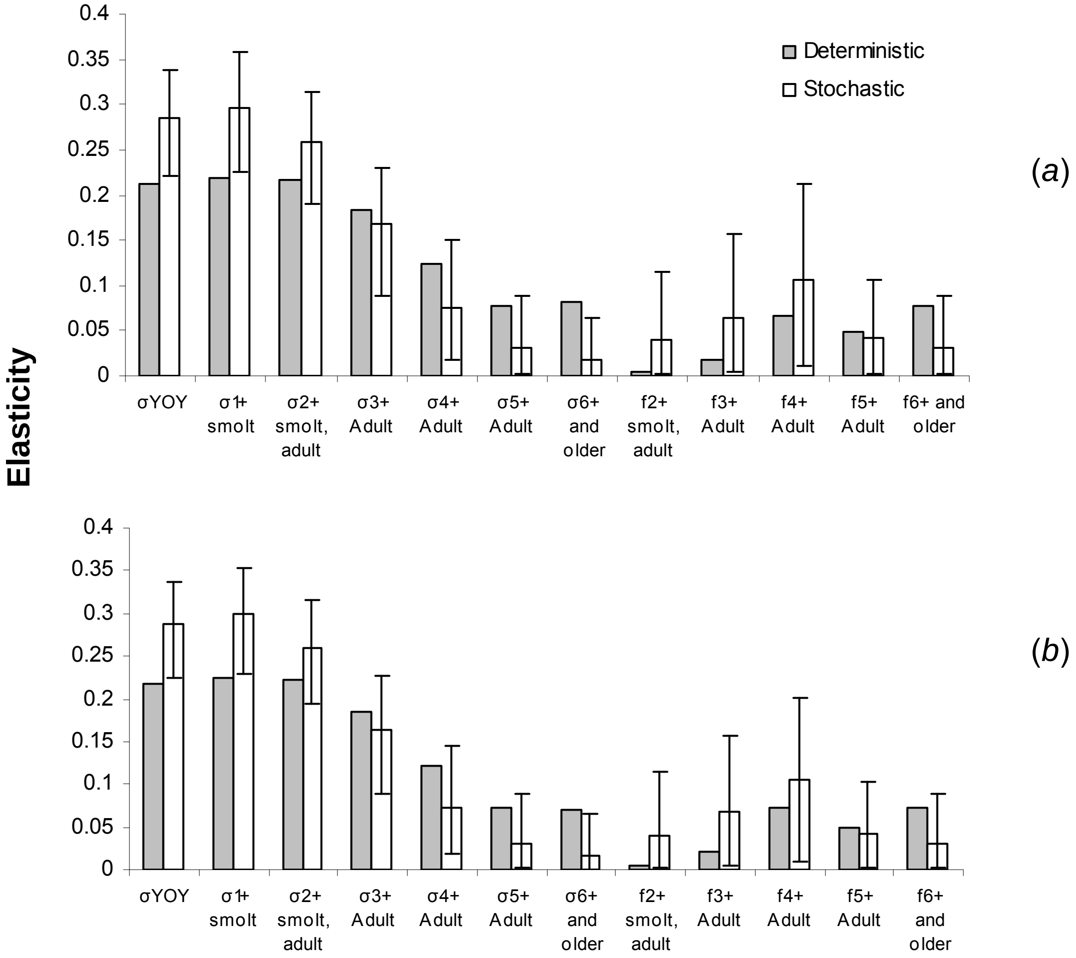


Figure 8. Deterministic and stochastic elasticity values for the survival probabilities of young-of-the-year (σ_{YOY}), one-year-old juvenile ($\sigma_{1+\text{ smolt}}$), two-year-old juvenile and two-year-old adult smolt ($\sigma_{2+\text{ smolt, adult}}$), three-year-old adult ($\sigma_{3+\text{ adult}}$), four-year-old adult ($\sigma_{4+\text{ adult}}$), five-year-old adult ($\sigma_{5+\text{ adult}}$), six-year-old and older adult ($\sigma_{6+\text{ and older}}$), and corresponding fertility rates (*f*). Error bars represent 95% confidence intervals. (*a*) Vital rate elasticities for a population growing at $\lambda = 1.024$. (*b*) Vital rate elasticities for a population declining at $\lambda = 0.99$.

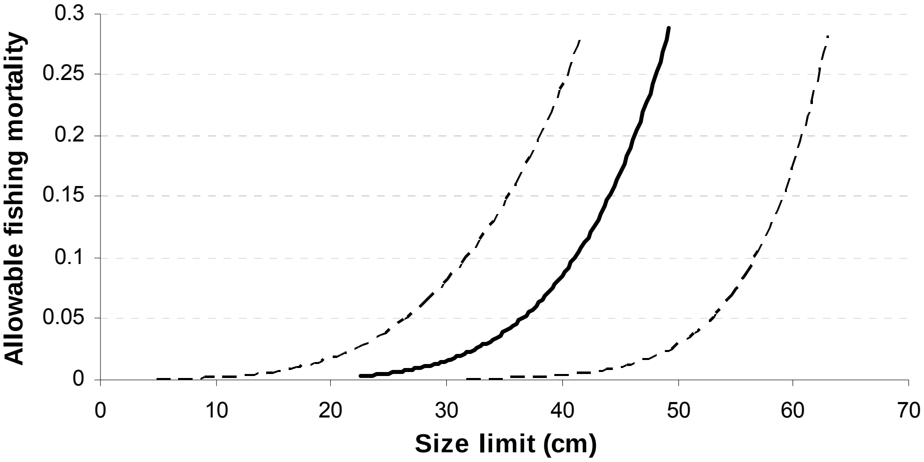


Figure 9. The relationship between maximum allowable fishing mortality (ω) and catch size limit in sport fisheries of landlocked Atlantic salmon. Continuous line represents mean length values. Dashed lines correspond to minimum and maximum total length at age.

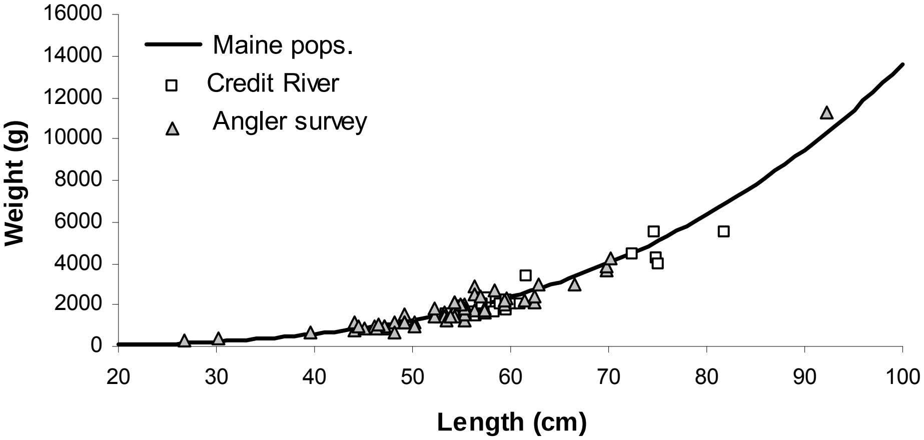


Figure 10. Length-weight data for the Credit River (1990-1991; n = 28) and angler surveys (1988-1994; n = 59) superposed on the regression curve for Maine populations.

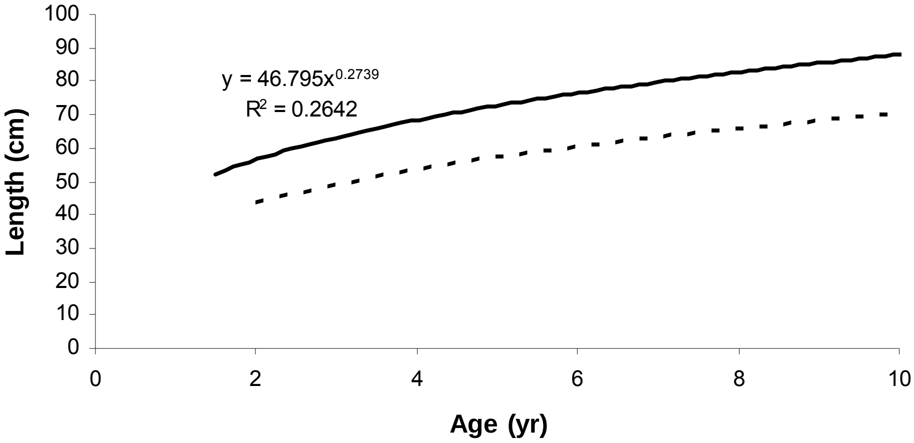


Figure 11. Length at age for Lake Ontario Atlantic salmon (solid line). Also shown is the growth pattern for maximum length at age from Maine populations.

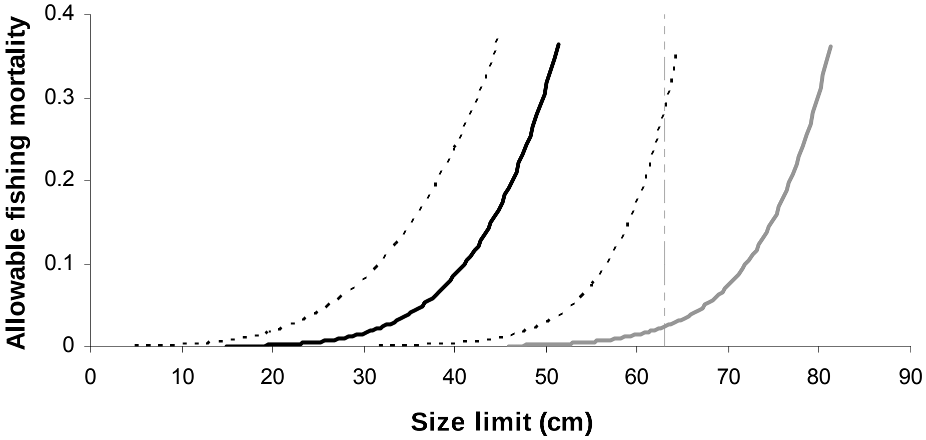


Figure 12. The relationship between maximum allowable fishing mortality and catch size limit in sport fisheries of landlocked Atlantic salmon representative of Maine populations (black lines) and the Lake Ontario population (grey line). Continuous lines represent mean length values. Dashed lines correspond to minimum and maximum total length at age (only shown for the Maine populations). Vertical line shows the current catch size limit.