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What is 2.4? Placing Atlantic Salmon Conservation Requirements in the Context of the Precautionary Approach to Fisheries Management in the Maritimes Region

À quoi correspond le chiffre 2,4? Remettre les exigences en matière de conservation du saumon de l'Atlantique dans le contexte de l'approche de précaution pour la gestion des pêches de la région des Maritimes

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ABSTRACT

The Department of Fisheries and Oceans (DFO) has adopted “A fishery decision-making framework incorporating the Precautionary Approach (PA)” that is to be used where decisions regarding commercial, recreational, or subsistence controls on harvest and all other removals are required.

For Atlantic salmon, the value of 2.4 eggs/m^2 of fluvial rearing habitat has a long history as a reference point in science and management advice. Here, this history is reviewed and the results of some newer population dynamics research that allows the conservation requirement to be placed in the context of the PA framework are summarized.

Although, in the past, reference points have been estimated for Atlantic salmon populations using a Ricker spawner-recruit function, this assumption was not tested. A comparison of spawner-recruit models for Atlantic salmon in the Maritimes region revealed no evidence of over-compensation and the Beverton-Holt model provided a significantly better fit when compared over all populations. Therefore, the Beverton-Holt model is the more appropriate spawner-recruit model for biomass-based reference points in the Maritimes Region. Although the value of 2.4 eggs/m^2 was originally proposed as a value for optimizing smolt production, it was modeled using Ricker spawner recruit functions and is not appropriate to be considered as an Upper Stock Reference in the PA framework.

In the Maritimes Region, the conservation requirement is consistent with a Limit Reference Point in the PA framework based on the empirical work defining 2.4 eggs/m^2 as the Atlantic salmon conservation requirement, its adoption by the Canadian Atlantic Fisheries Scientific Advisory Committee, and recent population dynamics research supporting the use of the Beverton-Holt relationship. The values for river-specific conservation requirements were estimated using consistent methods and are consistent with the framework advice on dealing with changes in productivity. Additionally, using these values as Limit Reference Points is supported by the current population dynamics work on the LaHave River (above Morgans Falls). The use of the estimated river-specific conservation requirements as Limit Reference Points for individual rivers in the Maritimes Region is recommended.

Additional research to refine Reference Points and Harvest Control Rules for fishery removals is not warranted given the current stock status and level of fish removals identified in recent Recovery Potential Assessments. Rather research on control rules guiding recovery action plans to limit mortality from other anthropocentric sources is required.

RÉSUMÉ

Pêches et Océans Canada a adopté « Un cadre décisionnel pour les pêches intégrant l'approche de précaution ». Il doit être appliqué en cas de prise de décisions au sujet du contrôle des prises de la pêche, qu'elle soit pratiquée à des fins commerciales, récréatives ou de subsistance, ou de tout autre type de prise.

La valeur 2,4 œufs/m^2 d'habitat de croissance fluvial est restée pendant longtemps, pour le saumon de l'Atlantique, le point de référence utilisé dans les recommandations scientifiques et de gestion. Cette publication reconsidère cette valeur et résume les résultats d'une recherche plus récente qui porte sur la dynamique des populations et replace les exigences de conservation dans le contexte du cadre de l'approche de précaution.

Auparavant, les points de référence pour les populations de saumon de l'Atlantique étaient estimés à l'aide du modèle de Ricker pour les reproducteurs-recrues, mais ce modèle n'a jamais été mis à l'essai. Une comparaison de modèles pour les reproducteurs-recrues du saumon de l'Atlantique dans la région des Maritimes n'a révélé aucune preuve de surcompensation, tandis que les résultats obtenus avec le modèle Beverton-Holt coïncident bien plus avec ceux des autres populations. Pour cette raison, le modèle Beverton-Holt est mieux adapté aux reproducteurs-recrues pour les points de référence basés sur la biomasse dans la région des Maritimes. Bien que la valeur 2,4 œufs/m^2 visait, à l'origine, à optimiser la production de saumoneaux, elle a été obtenue à l'aide du modèle de Ricker pour les reproducteurs-recrues et ne constitue donc pas un point de référence supérieur adapté dans le cadre de l'approche de précaution.

Dans la région des maritimes, l'exigence en matière de conservation est en accord avec le point de référence limite du cadre de l'approche de précaution, lui même établit en fonction des travaux empiriques établissant à 2,4 œufs/m^2 les exigences en matière de conservation du saumon de l'Atlantique, avec son adoption par le Comité scientifique consultatif des pêches canadiennes dans l'Atlantique, et avec les récentes recherches sur la dynamique des populations qui soutiennent l'utilisation du modèle Beverton-Holt. Les valeurs pour les exigences en matière de conservation dans les rivières ont été estimées à l'aide de méthodes cohérentes et sont conformes à l'avis du cadre concernant la gestion des changements de productivité. De plus, l'utilisation de ces valeurs comme point de référence est corroborée par les travaux en cours sur la dynamique des populations dans la rivière LaHave (située au-dessus des chutes Morgan). Il est recommandé de se servir des exigences de conservation estimées propres aux rivières comme point de référence limite pour les rivières de la région des Maritimes.

Compte tenu de l'état du stock et du niveau de prélèvements de poissons actuels qui ont été signalés dans les récentes évaluations du potentiel de rétablissement, il ne semble pas justifié de mener d'autres recherches visant à préciser les points de référence et les règles de contrôle des prises pour les prélèvements attribuables à la pêche. Il serait préférable d'entreprendre des travaux de recherche sur les règles de contrôle des prises servant à orienter les plans d'action en matière de rétablissement pour limiter la mortalité dans d'autres sources anthropocentriques.

INTRODUCTION

The Department of Fisheries and Oceans (DFO) has adopted “A fishery decision-making framework incorporating the Precautionary Approach (PA)” that is to be used where decisions regarding commercial, recreational, or subsistence controls on harvest and all other removal are required. The primary components of the PA (DFO 2006a) are:

1. Reference Points (RPs) and stock status zones (Healthy, Cautious and Critical).
2. Harvest strategies and harvest decision rules.
3. The need to take into account uncertainty and risk when developing reference points and developing and implementing decision rules.

The stock status zones are created by the Limit Reference Point (LRP) defining the critical to cautious boundary, an Upper Stock Reference (USR) defining the cautious to healthy boundary, and the removal reference for each of the three zones (DFO 2006a).

The LRP ideally represents the stock status below which serious harm occurs to the stock and is above the level where the risk of extinction is likely. Negative impacts to the ecosystem and long-term loss of fishing opportunities also influence the selection of the LRP. Serious harm in this context can result from either human-induced mortality or changes in population dynamics not related to human activities (DFO 2006a).

The USR defines the point at which removals must begin to be reduced in order to avoid reaching the LRP. To achieve this objective the USR must be high enough in comparison to the LRP to provide sufficient time for management actions to be implemented and to have the biological effect of promoting stock increases (DFO 2006a).

A Target Reference Point (TRP) may also be defined in the PA framework. It is defined to be equal to or greater than the USR and represents a stock status goal that the management system promotes (DFO 2006a).

The adoption of the LRP, USR, and TRP for any stock involves a combination of biological, social, and economic considerations. A completely non-arbitrary method of determining the specific abundance where serious harm will occur to a given stock does not exist. The arbitrariness arises from uncertainty in the biological data and changes in society’s perception of acceptable risk. Thus, biological, social, and economic considerations all carry weight in the definition of all these RPs. However, there is generally greater emphasis on biological considerations at the LRP and greater emphasis on the social and economic considerations at the TRP, and considerations for the USR fall somewhere in between depending on the particular fishery and the biological dynamics of the species (DFO 2006a).

A removal reference is also defined relative to the stock status zones as the maximum acceptable removal rate from all types of fishing. This rate in each of the three zones (Critical, Cautious and Healthy) should not exceed the removal reference in the healthy zone. The removal reference will vary depending on the stock’s location in each of the zones. It may also be influenced by factors other than those associated with stock status such as ecosystem effects, recruitment expectations, and other indicators of harvest pressures on a stock. As a result, adjustments of the removal reference in any zone do not have to be linear and the precise shape under any given circumstances will be determined during the establishment of Harvest Control Rules (HCRs) (DFO 2006a). Thus, it is important to distinguish those factors that describe stock status zones and those that describe effects resulting from changes in fishing pressure.

Harvest Control Rules are the strategies developed to manage the harvest of the stock under the PA framework. Although they are not discussed in this document, the stock status RPs create the basis for the development of these strategies based on discussions among the fishing industry, DFO fishery managers and scientists, and other stakeholders.

Productivity, whether from growth or recruitment, varies over time for all fish stocks and a given level will persist for varying lengths of time (Hilborn and Walters 1992). Identifying changes in productive regimes takes into account this variation. In general, reference points should not be established using only information from a particular productive regime unless there is no expectation that the stock will return to the previous regime. How shifts in productive regime would be determined in practice is not defined and the associated uncertainty with varying productivity is best accounted for by using as long a time-series as possible to define RPs (DFO 2006a).

The use of RPs in Atlantic salmon has a long history, although their application has been inconsistent (Chaput 2006). A value known as the conservation requirement, equating to an egg deposition value of 2.4 eggs/m^2 of fluvial rearing habitat (Elson 1957), has been most often used. However, it has also been used in the context of a target, limit, threshold, optimum spawning escapement, and conservation requirement throughout its history under various management scenarios and for various fisheries (Chaput 2006), leading to uncertainty in its interpretation.

In this research document, the history of the use of 2.4 eggs/m^2 as a RP for Atlantic salmon is reviewed, with an emphasis on populations in the Maritimes Region. In addition, the results of some newer population dynamics research that allows the conservation requirement to be placed in the context of the PA framework are summarized. This research includes two components: (1) the selection of appropriate stock recruitment models, a consideration not taken into account when the value of 2.4 was first determined, and (2) an equilibrium analysis of the dynamics of two Atlantic salmon populations, which allows comparisons of their conservation requirements to their unfished equilibrium biomass, to 20% of their unfished equilibrium biomass and to their Beverton-Holt half-saturation constant. The first of these values indicates the potential population size in the absence of human impacts, and is shown here for both the past and present time periods for the two Atlantic salmon populations. The latter two values have been proposed as minimum threshold population sizes for a variety of species (Beddington and Cooke 1983, Goodyear 1993, Myers et al. 1994, Caddy and McGarvey 1996).

It is concluded that both the definition of the conservation requirement and recent population dynamics research indicate that the value of 2.4 eggs/m^2 is consistent with an LRP in the PA framework.

REVIEW OF THE CONSERVATION REQUIREMENT FOR ATLANTIC SALMON

Elson (1957, 1975) took the view that maximizing smolt production was the most important objective for management of Atlantic salmon stocks. Based on work on the Miramichi River, New Brunswick, Canada and The River Foyle, Northern Ireland, he estimated that maximum smolt production would occur if adult salmon carrying the equivalent of 200 to 250 eggs/100yd^2 entered a river. This value incorporated uncertainty in management regimes by allowing for a 25% loss of adult salmon between entering the river and spawning. These levels would be needed to ensure an overall egg deposition rate of 140 eggs/100yd^2. He concluded that spawning numbers above these levels would likely result in a reduction of smolt production (Elson 1975).

In 1977, the Canadian Atlantic Fisheries Scientific Advisory Committee (CAFSAC) distinguished between optimum and maximum levels in reference to spawning requirements (Anon 1977). This work identified that the minimum number of spawners for maximum smolt production was 200 eggs/100yd^2 or 240 eggs/100m^2 (2.4eggs/m^2), and was the first link in the Canadian science advice for management that 2.4eggs/m^2 was the equivalent of a PA policy LRP.

Subsequent work focused on the maximum number of smolts that would be produced from different habitat types and populations with different life-history characteristics. These values ranged from 0.8 to 2.2 eggs/m^2 (Symons 1979). However, this level of detail was considered to be impractical for the general management of Atlantic salmon, and CAFSAC subsequently advised that levels of 2.0 eggs/m^2 were sufficient to conserve stocks and retain future options (Anon 1981). This conclusion was consistent with the PA definition of an LRP.

Considerable work occurred from 1980 to 1985 to update river-specific conservation requirements (LRPs) based on 2.4 eggs/m^2 (Porter and Chadwick 1983, Randall 1985, Randall 1984, Marshall and Penney 1983, Amiro and McNeill 1986). Predominantly, this work entailed the measurement and classification of habitat area in multiple watersheds. In the majority of rivers and regions, habitats with gradients >0.12% and <25% were included (O'Connell et al. 1997). However, subsequent work in Newfoundland demonstrated that lacustrine habitat should be considered productive in that region, so it was incorporated into the calculation of conservation requirements (LRP) for Newfoundland rivers (O'Connell and Dempson 1995, O'Connell et al. 2006).

In 1991, in response to legal challenges associated with food fisheries, CAFSAC reiterated that the conservation requirement based on 2.4 eggs/m^2 defined the spawning escapement below which no fishing should occur. CAFSAC (1991) considered the conservation requirement to be consistent with an LRP based on the definition of conservation from the United Nations Environment Program as:

> "That aspect of renewable resource management which ensures that utilization is sustainable and which safeguards ecological processes and genetic diversity for the maintenance of the resource concerned. Conservation ensures that the fullest sustainable advantage is derived from the resource base and that facilities are so located and conducted that the resource base is maintained." (CAFSAC 1991).

CAFSAC then adopted the specific reference level (i.e., 2.4 eggs/m^2) to allow assessment of whether conservation was being achieved:

> "CAFSAC, therefore, suggests as an operational translation of conservation the current target egg deposition rate of 2.4 eggs/m^2 of fluvial rearing habitat, and in addition for insular Newfoundland, 368 eggs/hectare of lacustrine habitat." (CAFSAC 1991).

The rationale provided for this reference level used terminology consistent with the definition of an LRP:

> "The 2.4 eggs/m^2 reference level is assumed to provide a modest margin of safety for some instream adult losses between the time salmon enter into a river and subsequent spawning, as well as for disproportionate adult exploitation and unequal rate of recruitment of the multiple stocks comprising a river stock complex. CAFSAC considers

> that the further the spawning escapement is below the biological reference level, and the longer this situation occurs even at rates only slightly below that level, the greater the possibility exists of incurring the following risks, some of which may cause irreversible damage to the stock: - accentuation of annual fluctuations in run size and reduction in the long-term capability of the stock to sustain native food fisheries, recreational fisheries, or commercial fisheries;
>
> 1. increased susceptibility to extinction from genetic, demographic, or environmental catastrophes and consequent decreases in productivity;
> 2. permanent changes in demographic characteristics of the spawning population;
> 3. replacement in the ecosystem by other competing fish species of potentially less social and economic value." (CAFSAC 1991).

Therefore, although the original derivation was consistent with a target reference level, the values of 2.4 eggs/m^2 of fluvial rearing habitat and 368 eggs/hectare of lacustrine habitat, were adopted as limits by CAFSAC (1991).

Although conservation requirements were established by CAFSAC (1991), river-specific values were not available for the majority of rivers in Atlantic Canada at that time. Subsequently, O'Connell et al. (1997) published the conservation requirements for many of the salmon rivers in eastern Canada, including in the Maritimes Region: 27 rivers in Salmon Fishing Area (SFA) 19 (Eastern Cape Breton), 27 rivers in SFA 20 (Nova Scotia's Eastern Shore), 19 rivers in SFA 21 (Southwestern Nova Scotia), 23 rivers in SFA 22 (the Nova Scotian portion of the inner Bay of Fundy [iBoF]), and 15 rivers in SFA 23 (the inner and outer Bay of Fundy rivers in New Brunswick). A workshop in 1997 supported the view that 2.4 eggs/m^2 be interpreted as a LRP (Chaput 1997).

While the values reported by O'Connell et al. (1997) were adopted as the conservation requirements for Atlantic salmon populations in the Maritimes Region, there were a few exceptions where alternate values were used in specific rivers for assessment. DFO (2011) pointed out two examples:

> "In the past, several methods have been used for estimating conservation requirements in rivers throughout Nova Scotia and New Brunswick. For most rivers, the values used are those reported in O'Connell et al. (1997) and are calculated as described in the Context section of this document. The conservation requirements being used for the LaHave [above Morgan's Falls] and St. Mary's rivers are lower than those reported in O'Connell et al. (1997), values of 6.3 million eggs and 9.6 million eggs, respectively." DFO (2011).

Values of 1.96 million eggs and 7.4 million eggs were being used.

The selection of values for the conservation requirement has consequences for the statements about status. For example, DFO (2011) then states:

> "If these values, which are calculated using methods that are consistent with the methods used for other rivers in the region, were used for these rivers, the resulting estimates of the percent of the conservation requirement achieved in 2010 would be lower for both rivers. On the St. Mary's River, the estimate would change from 5% to 4% of the conservation requirement attained on the West Branch of the River. On the LaHave River, the estimate would go from 35% to 11% of the conservation requirement attained above Morgan Falls." DFO (2011).

As shown in the next section for the Lahave River population, it is the value in O'Connell et al. (1997) that is consistent with both the Beverton-Holt half-saturation constant and 20% of the unfished equilibrium population size, not the lower value currently in use.

Although the value of 2.4 eggs/m^2 is widely used in Eastern Canada, other values have been adopted in some regions. For example, Caron et al. (1999) adopted an approach to defining the LRP that used Maximum Sustainable Yield (MSY) as the criteria and identified 1.67 eggs/Unit of Production as the LRP. However, the analysis by Caron et al. (1999) did not take into account the repeat spawning component present in many salmon populations, and thus would not be appropriate for populations in the Maritimes Region where repeat spawning is prevalent. Additionally, it was based on a Ricker spawner-recruit model without considering that other models (e.g., a Beverton-Holt or hockey-stick) might better describe the dynamics of Atlantic salmon populations.

Recently, the conservation requirement, expressed as an equivalent number of adults (values in Appendix 1), has been adopted as an interim recovery target for iBoF Atlantic salmon populations (DFO 2008), based in part on the CAFSAC definitions provided above. The equivalent number of adults for the 25 iBoF rivers for which the habitat amount has been quantified totals 9,919 fish. In comparison, the historical total abundance of iBoF salmon was estimated to be more than 40,000 fish. This use of the conservation requirement as a recovery target places the target at about one quarter the estimated past abundance of salmon in this area (DFO 2008). Additionally, historical abundance estimates from specific rivers often indicate that the requirement is not unduly large relative to past abundance. The approximate number of spawners equating to the conservation requirement for Stewiacke River is 772 small salmon and 289 large salmon. These values were exceeded most years from 1964 to 1985 (when both commercial and recreational fisheries were ongoing), at times by a factor greater than two. Similarly, pre-decline abundance on Big Salmon River, where the conservation requirements is 700 fish (280 small and 420 large salmon), at times exceeded 3,000 salmon, also when commercial fisheries were in operation (Gibson et al. 2008a). The conservation requirement was adopted as an interim recovery target because the dynamics of populations undergoing recovery are not known, making it difficult to determine the abundance at which extinction risk will become negligible or when human benefits can be derived from populations. However, DFO (2008) concluded that river-specific recovery targets are unlikely to be lower than the interim values, given the information about past abundance.

POPULATION DYNAMICS RESEARCH

In this section, recent research relevant to the selection of reference points (RPs) for salmon management is reviewed. First, work on the timing and nature of density dependence in Atlantic salmon is examined, questions that are fundamental for understanding the implications of management decisions for Atlantic salmon (Hindar et al. 2011). Secondly, some analyses of the dynamics of Atlantic salmon populations that allow the conservation requirement to be placed in the context of the LRPs and USRs for the precautionary framework are reviewed.

NATURE OF DENSITY DEPENDENCE

Knowledge of the timing and nature of density dependence is fundamental for deriving model-based RPs for fisheries management. The original analyses of Elson (1975) and the subsequent analyses of Caron et al. (1999) are based on the concept that there is an optimum spawner abundance above which recruitment declines (termed over-compensation), yet neither paper provides support for the assumption that this optimum exists. Therefore, it is important to determine whether Atlantic salmon population dynamics are purely compensatory (and would be appropriately described by a model like the Beverton-Holt spawner recruitment model) or whether over-compensation is characteristic of their dynamics (in which case a Ricker model would be appropriate).

Gibson (2006) undertook an analysis of the timing and nature of density dependent survival in Atlantic salmon using electrofishing data from nine populations in the Maritime Provinces to evaluate its role in freshwater environments, and smolt-to-adult return-rate data from 15 populations in eastern Canada to evaluate its importance in marine habitat. Gibson (2006) fit three spawner-recruit models to each data series, a Beverton-Holt, a Ricker and a one-parameter density-independent model using maximum likelihood, and compared model fits using likelihood ratio tests. Within fresh water, no single, unequivocal pattern was evident with respect to the timing of density dependence, although density dependence characterized the dynamics of all the modeled populations. In the marine environment, density dependence was potentially detected in three of the 15 return-rate data series for salmon maturing after one winter at sea, but was not detected in any of the nine return-rate data series for fish maturing after two winters at sea.

Importantly in the context of estimating RPs, over-compensation was not detected in these data. The Ricker model (which exhibits over-compensation) did not provide a better statistically significantly fit in any of the 24 comparisons, made over all populations, the Beverton-Holt model (which does not exhibit over-compensation) provided a better fit that was statistically significant when compared across all populations (Table 1).

Also relevant to the issue of estimating RPs, Gibson (2006) found that the carrying capacity for age-1 salmon was highly variable among populations, with the implication that LRPs would also be highly variable among populations. Using a mixed-effects model, the median carrying capacity was estimated to be 24.8 parr/100m^2 with 95% of the probability density falling between 3.8 and 165.9 parr/100m^2 (Figure 1). Hindar et al. (2011) asked the question why carrying capacity would be so variable based on the analysis of Gibson (2006). There are at least two reasons. First, the physical characteristics and underlying geology of rivers would cause variation in habitat quality among rivers. Second, the extent to which humans have impacted on Atlantic salmon populations also varies among rivers. For example, within the Southern Upland region (Nova Scotia’s Atlantic coast), rivers range from relatively un-impacted by acid rain to those in which water quality is so poor that salmon cannot survive. Hydropower generation and land use are other issues known to affect productivity, and the river with the lowest estimated carrying capacity shown in Figure 1 is the Tobique River, which is impacted by both of these activities. Although population dynamics models for the Tobique population exist (Gibson et al. 2009), it would not be appropriate to use these models for estimating RPs unless the anthropogenic impacts upon the population were somehow included in the model. Therefore, although having river-specific reference levels would be desirable given the variability in the habitat carrying capacity among rivers, it is currently impractical given both the large number of rivers for which there is no data to estimate carrying capacity, as well as the difficulties is separating natural variability in carrying capacity from variability resulting from human activities impacting on some populations, but not others.

Overall, the analyses of Gibson (2006) strongly support the spawner-recruit function used in the dynamics models described below. They provide strong evidence that over-compensation is not a characteristic of Atlantic salmon populations in the Maritimes region. This provides insight into why an optimum for smolt production does not exist. In the absence of over-compensation, smolt production is maximized at an infinite egg deposition, not at an intermediate abundance level. Although the original analysis used to derive the reference level of 2.4 eggs/m^2 was based on an egg deposition to optimize smolt production, the inappropriateness of the spawner-recruit function helps to explain why the derived value can now be considered an LRP rather than a USR.

PLACING 2.4 EGGS/M^2 IN THE CONTEXT OF THE PRECAUTIONARY FRAMEWORK

Population dynamics models using equilibrium approaches have been developed and used as the basis for advice for five populations in the Maritimes Region: the Tobique (DFO 2006b, Gibson et al. 2007, Gibson et al. 2009) and Big Salmon (Gibson et al. 2008a,b) rivers in New Brunswick; and the LaHave (Gibson et al. 2009, Gibson and Bowlby 2013), St. Mary's (Gibson et al. 2009, Gibson and Bowlby 2013) and West (Gibson et al. 2008a) rivers in Nova Scotia.

Equilibrium models are versatile and have been widely used for estimating biological RPs for fisheries management (e.g., Sissenwine and Shepherd 1987, Gibson and Myers 2004), for predicting the long-term consequences of mortality caused by pollution, dams or other human activities (e.g., Barnthouse et al. 1988), and for linking fish habitat and fish population dynamics (e.g., Hayes et al. 1996). The modeling approach is described in full by Gibson et al. (2009) and Gibson and Bowlby (2013). In brief, the life cycle of a species is split into two parts, each characterized by a measure of productivity that is influenced by one or several life history parameters (such as fecundity, age- or stage-specific survival, age-at-maturity or reproductive rate or frequency). The equilibrium population size occurs where the productivity of both halves of the life cycle are balanced such that the population does not increase or decrease in size. For the populations mentioned above, life history parameter estimates are obtained either by fitting the model to the available population-specific data (e.g., egg deposition estimates, juvenile density data obtained by electrofishing, smolt abundance data, counts of adults ascending ladders, age data) using maximum likelihood, or are "borrowed" from nearby populations thought to be representative. Output from the model include abundance time-series for each life stage and age category, estimates of fishing and natural mortality, carrying capacity, the maximum lifetime reproductive rate, Beverton-Holt spawner-recruit parameters and the unfished equilibrium population size.

To determine whether the population dynamics of Atlantic salmon in the Maritimes Region support the idea that egg depositions equivalent to 2.4 eggs/m^2 are consistent with an LRP, this value is compared to two LRPs proposed in the literature: 20% of the unfished equilibrium biomass ($B_{20\%}$) and the Beverton-Holt half-saturation constant (*k*). For salmon, number of eggs are used as the metric rather than biomass, which should be appropriate given that biomass is typically used as a proxy for fecundity. Beddington and Cooke (1983) proposed $B_{20\%}$ as a minimum threshold population size, and this value is consistent with other limit reference points proposed for other species under the PA. For example, if a symmetrical Schaeffer surplus production model is used, B_{msy} equates to 50% of the unfished equilibrium population size. An LRP of 40% of B_{msy} has been proposed under the PA, which equates to 20% of the unfished equilibrium (i.e., $B_{20\%}$). While surplus production curves for Atlantic salmon are likely not symmetrical, this example does help place $B_{20\%}$ in the context of other proposed LRPs under the PA. The other proposed minimum threshold being used for comparison is the Beverton-Holt half-saturation constant. This is the level of spawner abundance at which recruitment is half the maximum. In this context, it is a "threshold" biomass that the spawning biomass should not come close to (Myers et al. 1994).

Of the five populations for which equilibrium models have been developed, there are two that have the characteristics necessary to estimate LRPs: the Big Salmon River in New Brunswick and the Lahave River (above Morgans Falls) in Nova Scotia. Equilibrium models for both of these rivers have been developed from population-specific data exclusively. Additionally, these are rivers where habitat issues are not thought to be significantly influencing smolt production and thus the unfished equilibrium population size. Estimates of population dynamics parameters during past and more recent time periods are provided in Table 2 and equilibrium plots of the population dynamics are shown in figures 2 and 3. At present, maximum lifetime reproductive rates are less than one for both populations, indicating that neither population is viable under current conditions (equilibrium population sizes of zero). In the past, equilibrium population sizes were 23.1 and 14.2 million eggs for the Lahave and Big Salmon populations, respectively.

In comparison with the two alternate reference levels proposed above, the conservation requirement (based on an egg deposition of 2.4 eggs/m^2) is slightly greater than $B_{20\%}$ but is less than *k* for the LaHave River, and is less than both $B_{20\%}$ and *k* on the Big Salmon River. This strongly suggests that the conservation requirement is more in line with an LRP than an upper reference level in the PA. The estimate of the alpha parameter (the Beverton-Holt slope at the origin) for the Big Salmon population intuitively appears low (5 smolts per 100 eggs), so the possibility that alpha is being underestimated in the model cannot be discounted. If this is occurring, then the parameter *k* may be overestimated, biasing comparisons with the conservation requirement.

SUMMARY AND CONCLUSIONS

1. Although RPs have been estimated for Atlantic salmon populations using a Ricker spawner-recruit function in the past, this assumption was not tested. There is no evidence of over-compensation occurring in Atlantic salmon populations in the Maritimes Region. Therefore, biomass-based RPs in the Maritimes are more appropriately derived using the Beverton-Holt spawner-recruit model.

2. Thus, the value of 2.4 eggs/m^2 of fluvial rearing habitat, originally proposed as a value for optimizing smolt production, was modeled using the Ricker spawner-recruit function and is not appropriate to be considered as an USR.

3. The empirical work defining 2.4 eggs/m^2 as the Atlantic salmon conservation requirement, its adoption by CAFSAC, and recent population dynamics research supporting the Beverton-Holt relationship indicate that, in the Maritimes Region, the conservation requirement is consistent with an LRP in the precautionary framework.

4. The values in O'Connell et al. (1997) are estimated using consistent methods and are consistent with the framework advice on dealing with changes in productivity. Using these values as LRPs is supported by the current population dynamics work on the LaHave River (above Morgans Falls).

5. Values in O'Connell et al. (1997) should be used as individual river LRPs for the Maritimes Region (Appendix 1).

6. Additional research to refine RPs and HCRs for fishery removals in this region is not warranted given the current stock status. Rather research in support of recovery action plans to limit mortality from anthropocentric sources other than fisheries is required.

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Table 1. Comparison of the negative log-likelihoods obtained by fitting Beverton-Holt and Ricker models to juvenile salmon data for nine populations in the Maritime Provinces (from Gibson 2006).

Life Stage Transition	River	Beverton-Holt	Ricker
egg-to-age-0	Big Salmon River	71.087	74.431
	Nashwaak River	30.773	30.991
	NW Miramichi River	51.768	54.679
	St. Mary's River	28.940	29.065
	SW Miramichi River	54.857	54.590
	Tobique River	39.955	39.859
egg-to-age-0 total		**277.381**	**283.615**
age-0-to-age-1	Big Salmon River	42.761	43.445
	Margaree River	30.859	30.832
	Nashwaak River	52.080	56.401
	NW Miramichi River	112.952	113.901
	Restigouche River	81.045	81.940
	St. Mary's River	29.185	29.349
	Stewiacke River	42.840	42.834
	SW Miramichi River	102.027	101.920
	Tobique River	35.452	40.752
age-0-to-age-1 total		**529.201**	**541.374**
age-1-to-age-2	Big Salmon River	30.007	30.518
	Margaree River	25.712	25.811
	Nashwaak River	22.151	22.528
	NW Miramichi River	61.813	63.306
	Restigouche River	45.039	45.039
	St. Mary's River	3.929	3.785
	Stewiacke River	20.186	20.237
	SW Miramichi River	45.157	46.396
	Tobique River	14.318	14.382
age-1-to-age-2 total		**268.312**	**272.002**

Table 2. A comparison of the conservation requirement for Atlantic salmon in the LaHave River (above Morgans Falls), Nova Scotia (NS), and the Big Salmon River, New Brunswick (NB), with proposed limit reference points and reference levels being used to implement the precautionary approach to fisheries management. All reference points are presented in millions of eggs. Adapted from Gibson et al. (2008b) and Gibson and Bowlby 2013.

	LaHave River above Morgans Falls		Big Salmon River.	
	1980-1989	2000-2009	1967-1971	2001-2004
Conservation Requirement (millions of eggs)	6.25 million eggs		2.18 million eggs	
Asymptotic recruitment level (1000's of smolts)	147,000	134,000	56,000	56,000
Alpha (smolts/egg)	0.016	0.013	0.005	0.005
Lifetime Eggs per smolt	217	63	438	115
Max. lifetime reproductive rate (spawners per spawner)	3.59	0.84	2.19	0.57
k (number of eggs)	9.2 million	10.3 million	10.2 million	10.2 million
B_0 (number of eggs)	23.1 million	0.0	14.2 million	0.0
$B_{20\%}$ (number of eggs)	4.6 million	0.0	2.8 million	0.0

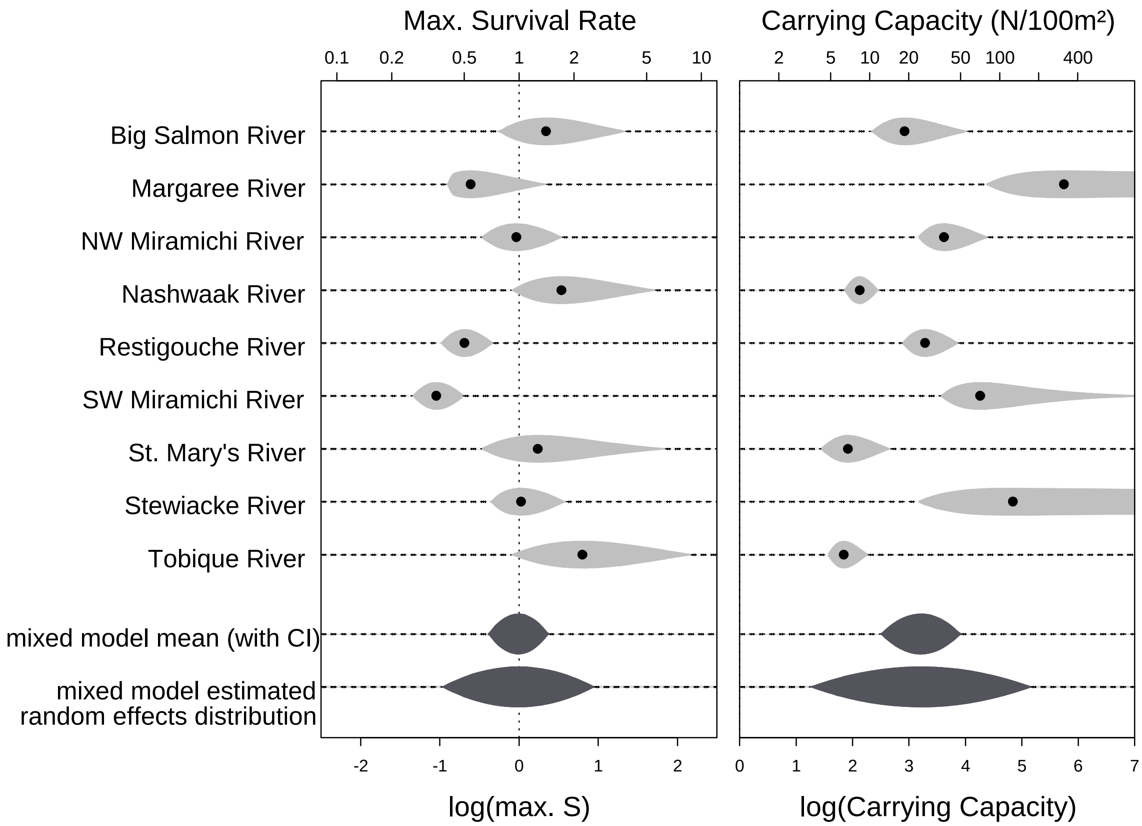

Figure 1. A meta-analytic summary of the maximium age-0-to-age-1 survival rate and the habitat carrying capacity for age-1 parr for nine salmon populations. The light grey shaded regions are individual fits that depict the profile likelihood for each parameter, truncated to show the 95% confidence interval. The height of the profile is used to gauge the relative plausibility of different values (greater height is more plausible). The black dot is the maximum likelihood estimate for each parameter. The dark grey shaded regions show summaries of the mixed model results. The "mixed model mean" represents the estimated mean of the logarithm of each parameter with a 95% confidence interval. The "mixed model estimated random effects distribution" is the normal distribution for the logarithm of each parameter based on its mean and variance estimated with the mixed-effects model (from Gibson 2006).

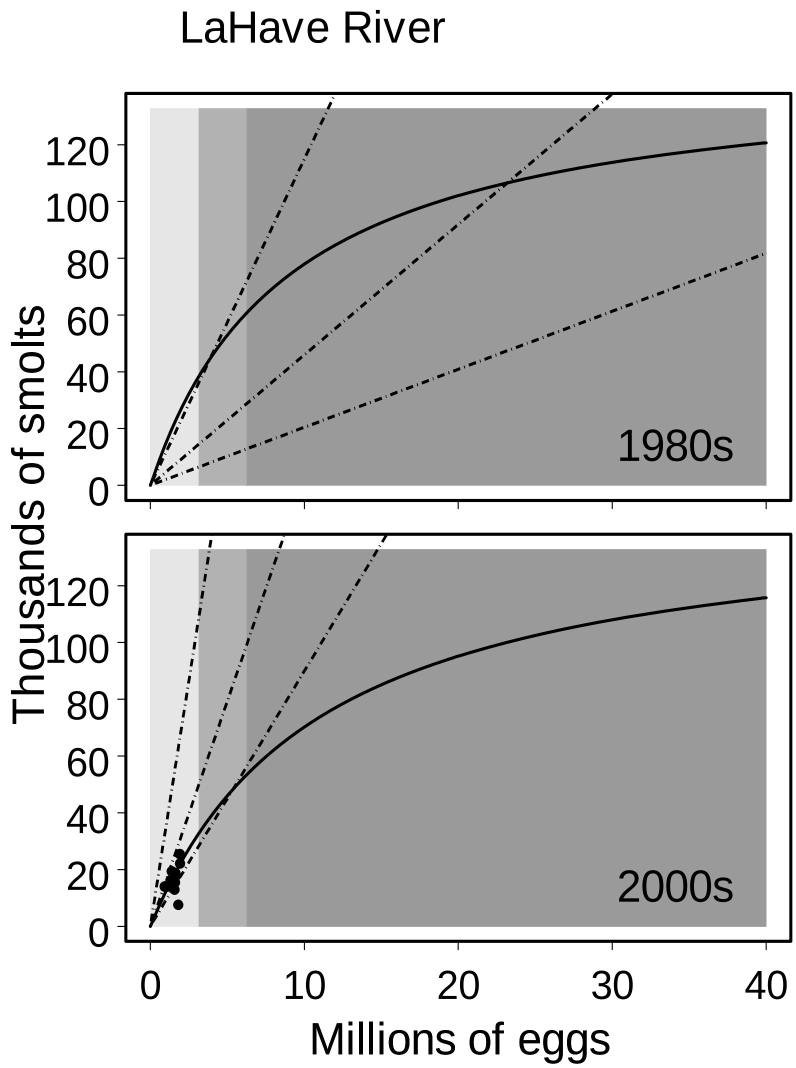

Figure 2. Equilibrium analysis of the salmon population dynamics in the LaHave River, NS, above Morgan Falls. The points are the observed egg depositions and smolt production for the 1980 to 1989 (top panel) and the 2000 to 2008 (lower panel) egg deposition years. The curved, solid line represents freshwater 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. (from Gibson and Bowlby 2013).

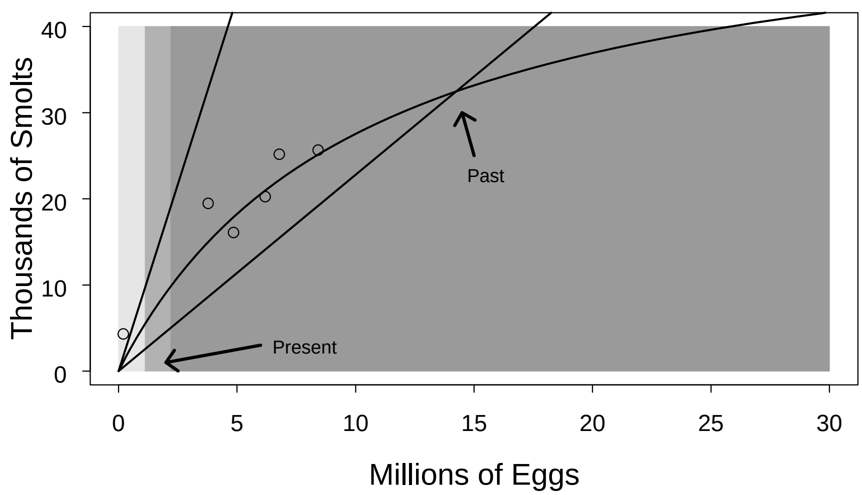

Figure 3. Equilibrium analysis for salmon of the Big Salmon River, NB, showing the change in equilibrium population size resulting from a decrease in at-sea survival between two time periods, the past (1967-1971) and present (2001-2004). The solid curved line shows the freshwater production that results when a life history model is fit to all available data. The two straight lines are the replacement lines calculated using the past and present dynamics estimated using the same life history model. Shading indicates the status relative to the conservation egg requirement: dark shading is above the requirement, the medium shading is between 50% and 100% the egg requirement and the light shading is below the requirement (adapted from Gibson et al. 2008b).

Appendix 1. Drainage areas, rearing habitat areas, and the egg requirement (LRP) based on an egg deposition of 2.4 eggs/m^2 of fluvial rearing habitat for Maritimes Region rivers (from O'Connell et al. 1997). The numbers of fish expected to produce this egg deposition are also shown. Reference footnotes are in O'Connell et al. (1997). Note that the egg requirement is the LRP. The numbers of adult salmon are provided as a rough guide to the corresponding population size.

SFA	River name	Drainage area (sq. km)	Rearing units (100 sq. m)	R. units per sq. km	Egg requirement (240/unit)	Spawner requirement (No.) Small salmon	Large salmon	Total	Prop. 2SW	2SW	References
SFA 19	(Atlantic Cape Breton)										
	Aconi Brook		1045		250800	8	45	52			7,2-Sydney
	Baddeck		8363		2007120	80	450	530			7,2-Baddeck,8
	Barachois		5979		1434960	57	322	379			7,2-Baddeck
	Catalone		4311		1034640			509			7,2-Grand
	Clyburne	70	1165	16.7	279594	10	65	75			1,2-North
	Framboise		6698		1607520			790			7,2-Grand
	Gerrat Brk		842		202080	7	47	54			7,2-North
	Grand		4618		1108320			545			7,2-Grand,9
	Indian Brk (Eskasoni)		1007		241680	8	57	65			7,2-North
	Ingonish		1934		464160	16	109	125			7,2-North
	Inhabitants		5889		1413360	44	252	296			7,2-Sydney
	Little Lorraine Brk	37	718	19.6	172355	5	31	36			1,2-Sydney
	Lorraine Brk		2611		626640	19	112	131			7,2-Sydney
	MacAskills Brook	50	840	16.7	201606	6	36	42			1-North,2-Sydney
	Marie Joseph		4231		1015440	36	238	273			7,2-North
	Middle		8646		2075040	80	470	550			7,2-Middle,8
	North Aspy	168	2807	16.7	673721	24	158	181			1,2-North
	North		3827		918480	32	215	247			7,2-North,8,10
	Northwest Brk (River Ryan)	53	1031	19.6	247369	9	58	67			1-Sydney,2-North
	River Bennett	24	469	19.6	112515	4	26	30			1-Sydney,2-North
	River Deny's	214	4196	19.6	1006952	39	179	218			1-Sydney,2-Middle
	Salmon River (Victoria Co.)	219	3657	16.7	877692	31	206	236			1,2-North
	Salmon/Gasperaux		6790		1629600	51	539	590			7,2-Sydney
	Skye	116	1945	16.7	466896	18	106	124			1-North,2-Middle
	Sydney		3615		867600	27	155	181			7,2-Sydney,11
	Tillard		1129		270960	8	48	57			7,2-Sydney
	Total SFA 19		**88363**		**21207100**	**620**	**3922**	**6386**	**0.80**	**3138**	prop-blended

Appendix 1 (continued).

SFA	River name	Drainage area (sq. km)	Rearing units (100 sq. m)	R. units per sq. km	Egg requirement (240/unit)	Spawner requirement (No.) Small salmon	Large salmon	Total	Prop. 2SW	2SW	References
SFA 20	(Eastern Shore NS)										
	Chezzetcook		1852		444480	244	21	265			12,7,2-Liscomb
	Clam Harbour		2736		656640	360	31	391			12,7,2-Liscomb
	Cole Harbour		1244		298560	164	14	178			12,7,2-Liscomb
	Country Harbour		3270		784800	430	38	468			7,2-Liscomb
	East Sheet Harbour		29749		7139760	3914	342	4256			12,7,2-Liscomb
	Ecum Secum		7663		1839120	1008	88	1096			12,7,2-Liscomb
	Gaspereau Brook		2823		677520	371	32	404			7,2-Liscomb
	Guysborough		4217		1012080	555	48	603			7,2-Liscomb
	Halfway Brook		1604		384960	211	18	229			12,7,2-Liscomb
	Isaac's Harbour		2043		490320	269	23	292			12,7,2-Liscomb
	Larry's		2410		578400	317	28	345			12,7,2-Liscomb
	Lawrencetown Lake (Salmon R.)		6446		1547040	848	74	922			12,7,2-Liscomb
	Liscomb		16856		4045440	2218	194	2412			12,13-Liscomb+St. Mary's
	Little Salmon (Lk Major)		750		180000	99	9	107			12,7,2-Liscomb
	Moser		15208		3649920	2001	175	2176			7,2-Liscomb
	Musquodoboit		7919		1900560	846	204	1050			7,2-LaHave
	New Harbour		3148		755520	414	36	450			12,7,2-Liscomb
	Port Dufferin		5389		1293360	709	62	771			12,7,2-Liscomb
	Porters Lake (East Brook)		2332		559680	307	27	334			12,7,2-Liscomb
	Quoddy		6849		1643760	901	79	980			7,2-Liscomb
	Saint Mary's		39854		9564960	3155	889	4044			7,2-St. Mary's
	Salmon: Guysborough Co.		11789		2829360	1551	136	1687			7,2-St. Mary's
	Salmon: Halifax Co.		2811		674640	370	32	402			12,7,2-Liscomb
	Ship Harbour Lake Charlotte		19615		4707600	2581	226	2806			7,2-Liscomb
	Tangier		13583		3259920	1787	156	1943			12,7,2-Liscomb
	West Porters Lake		1185		284400	156	14	170			12,7,2-Liscomb
	West Sheet Harbour		16672		4001280	1163	132	1295			12,7,2-Liscomb,14
	Total SFA 20		**230017**		**55204080**	**26948**	**3129**	**30077**	**0.86**	**2691**	prop-Liscomb

Appendix 1 (continued).

SFA	River name	Drainage area (sq. km)	Rearing units (100 sq. m)	R. units per sq. km	Egg requirement (240/unit)	Spawner requirement (No.) Small salmon	Large salmon	Total	Prop. 2SW	2SW	References
SFA 21	(South Shore NS)										
	Barrington		4999		1199760	534	128	663			12,7,2-LaHave
	Clyde		24256		5821440	2592	623	3216			12,7,2-LaHave
	East(Lun)		3969		952560	424	102	526			7,2-LaHave
	Gold		17741		4257840	1896	456	2352			7,2-LaHave
	Hubbards		923		221520	99	24	122			7,2-LaHave
	Ingram		3702		888480	396	95	491			7,2-LaHave
	Jordan		15777		3786480	1686	406	2092			12,7,2-LaHave
	LaHave		50848		12203520	5434	1307	6741			7,2-LaHave
	Martins		5441		1305840	581	140	721			7,2-LaHave
	Medway		67653		16236720	7230	1739	8969			7,2-LaHave
	Middle		9270		2224800	991	238	1229			7,2-LaHave
	Mushamush		2303		552720	246	59	305			7,2-LaHave
	Nine Mile		3334		800160	356	86	442			12,7,2-LaHave
	Petite		6444		1546560	689	166	854			7,2-LaHave
	Roseway		17792		4270080	1901	457	2359			12,7,2-LaHave
	Sable		8869		2128560	948	228	1176			12,7,2-LaHave
	Sackville		6485		1556400	693	167	860			7,2-LaHave
	Salmon (Digby)		7727		1854480	826	199	1024			7,2-LaHave
	Tusket		65764		15783360	7028	1690	8718			7,2-LaHave
	Total SFA 21		**323297**		**77591280**	**34550**	**8310**	**42860**	**0.70**	**5817**	prop-LaHave

Appendix 1 (continued).

SFA	River name	Drainage area (sq. km)	Rearing units (100 sq. m)	R. units per sq. km	Egg requirement (240/unit)	Spawner requirement (No.) Small salmon	Large salmon	Total	Prop. 2SW	2SW	References
SFA 22	(Inner-Fundy NS)										
	Annapolis		20886		5012640	2232	537	2769	0.70	376	7,2-LaHave
	Apple		2111		506640	125	47	171	0.03	1	7,2-Stewiacke
	Bass (Colchester Co.)		696		167040	41	15	56	0.03	0	7,2-Stewiacke
	Chiganois		3369		808560	199	74	273	0.03	2	7,2-Stewiacke
	Cornwallis		1706		409440	182	44	226	0.70	31	7,2-LaHave
	Debert		3499		839760	206	77	284	0.03	2	7,2-Stewiacke
	Diligent		335		80400	20	7	27	0.03	0	7,2-Stewiacke
	Economy		2386		572640	141	53	193	0.03	2	7,2-Stewiacke
	Folly		2896		695040	171	64	235	0.03	2	7,2-Stewiacke
	Gaspereau (Kings Co.)		3856		925440	412	99	511	0.70	69	7,2-LaHave
	Great Village		2587		620880	153	57	210	0.03	2	7,2-Stewiacke
	Harrington		629		150960	37	14	51	0.03	0	7,2-Stewiacke
	Kennetcook		3976		954240	235	88	322	0.03	3	7,2-Stewiacke
	Maccan		8228		1974720	485	182	667	0.03	5	7,2-Stewiacke
	North (Colchester Co.)		4485		1076400	265	99	364	0.03	3	7,2-Stewiacke
	Parrsboro		705		169200	42	16	57	0.03	0	7,2-Stewiacke
	Portapique		3309		794160	195	73	268	0.03	2	7,2-Stewiacke
	River Hebert		2282		547680	135	50	185	0.03	2	7,2-Stewiacke
	Salmon (Colchester Co.)		13468		3232320	795	297	1092	0.03	9	7,2-Stewiacke
	Shubenacadie		10340		2481600	610	228	838	0.03	7	7,2-Stewiacke
	St. Croix (Hants Co.)		4283		1027920	253	95	347	0.03	3	7,2-Stewiacke
	Stewiacke		13086		3140640	772	289	1061	0.03	9	7,2-Stewiacke,15,16
	Tantramar		-								
	Total SFA 22		**88232**		**21175680**	**5471**	**1969**	**7440**	**0.03**	**531**	prop-Stewiack, LaHave

Appendix 1 (continued).

SFA	River name	Drainage area (sq. km)	Rearing units (100 sq. m)	R. units per sq. km	Egg requirement (240/unit)	Spawner requirement (No.) Small salmon	Large salmon	Total	Prop. 2SW	2SW	References
SFA 23	(Inner-Fundy NB)										
	Demoiselle Crk										
	Crooked Crk										
	Shepody										
	West (Albert Co.										
	Alma					60	29	89			15
	Point Wolfe					139	63	202			15
	Petitcodiac		28150		6756000	1688	101	1789			17
	Big Salmon		9093		2182320	280	420	700			7,2-Big Salmon,8,18
	Irish										
	Mosher (Saint John Co.)										
	Subtotal		37243		8938320	2167	613	2780	0.13	80	prop-Big Salmon
SFA 23	(Outer-Fundy NB)										
	Digdeguash		4220		1012800	100	170	270			5, App VI-14 p170
	Magaguadavic		5630		1351200	140	230	370			5, App VI-14 p170
	Saint John above Mactaquac		134722		32333280	4900	4900	9800			7,2-Saint John,19
	Saint John below Mactaquac		199740		47937600	7400	7400	14800			7,2-Nashwaak trib,19
	St. Croix		30790		7389600	680	1710	2390			20
	Others		2350		564000	60	100	160			5, App VI-14 p170
	Subtotal		377452		90588480	13280	14510	27790	0.90	13059	prop-Saint John
	Total SFA 23		**414695**		**99526800**	**15447**	**15123**	**30570**		**13139**	

1-Drainage area from Maritime Resource Management Service, rearing units per sq. km from 'named' river; 2-Spawners from 'named' river; 3-Edwards (MS 1956); 4-Chaput and Jones (MS 1994) 5-Anon.(MS 1978); 6-Marshall (MS 1982); 7-Rearing units > 0.12% ortho-gradient measured on air photos (Amiro 1993); 8-Marshall et al. (MS 1992); 9- Amiro and Longard (MS 1990); 10-Amiro and Marshall (MS 1990); 11-Marshall et al. (MS 1996); 12- Significant acidification; 13-Semple and Cameron (MS 1990); 14-Liscomb proportion at age data, 1992-95; 15-Amiro and Jefferson (MS 1996); 16-Amiro (MS 1990); 17- Semple (MS 1984); 18- Amiro and McNeill (MS 1986); 19- Marshall and Penney (MS 1983); 20-Anon. (MS 1988b).