Elements in the development of conservation plans for Atlantic salmon (*Salmo salar*)

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Abstract: This paper examines two areas to be considered in developing conservation plans for Atlantic salmon (*Salmo salar*): goal statements and the general framework for the implementation of a conservation plan. From a biological perspective, the appropriate conservation unit for Atlantic salmon is the Evolutionary Significant Unit (ESU). As conservation decisions will rarely be based solely on biological information, the Operational Conservation Unit (OCU) is defined as resulting from the interplay between biological requirements and socio-economic issues. A multi-scale habitat inventory of Atlantic salmon rivers to know what their status is relative to historical conditions is the first step in a functional conservation plan. The viability of salmon populations may be assessed according to 6 variables: abundance, resilience, age and size structure, sex ratio, spatial and geographical distribution. A genetically viable population possesses the species' evolutionary legacy and the genetic variation on which future evolutionary potential depends. Four factors important to monitoring changes in a population's genetic health are genetic diversity, effective population size, genetic bottlenecks and founder effects and gene flow. Implementation of a conservation plan must be proactive to maintain the quality of the OCUs. Commercial and recreational fisheries need to be limited and several case studies are reviewed. The importance of avoiding the introduction of exotics and minimizing the impact of sampling methodology, as well as the pitfalls of planting eggs, fry, or parr, are addressed. Finally, the importance of fostering public awareness of the value of conservation is essential to apply the political pressure necessary to preserve natural resources.

Résumé : Cet article traite de deux éléments qui doivent être considérés dans l'élaboration des plans de conservation du saumon de l'Atlantique (*Salmo salar*) : l'énoncé des objectifs et le cadre général de mise en oeuvre du plan. Du point de vue biologique, l'unité de conservation appropriée pour le saumon atlantique est l'unité évolutionnaire significative. Comme les décisions en matière de conservation sont rarement fondées sur les seules données biologiques, on a aussi recours à la notion d'unité opérationnelle de conservation qui tient compte de l'interaction entre les exigences biologiques et les questions socio-économiques. La première étape d'un plan fonctionnel de conservation consiste à réaliser un inventaire à échelles multiples des habitats des rivières à saumon atlantique pour comparer l'état actuel des habitats à leur état passé. La viabilité des populations de saumon peut être évaluée en fonction de six variables : l'abondance, la résilience, la structure par âge et par taille, la proportion des sexes et la répartition spatiale et géographique. Une population génétiquement viable possède le patrimoine évolutionnaire de l'espèce et la variabilité génétique desquels dépend le potentiel évolutionnaire futur. La diversité génétique, la taille effective de la population, les goulots d'étranglement génétique et les effets génétiques du fondateur, et enfin le flux génétique sont quatre facteurs importants dans la surveillance des changements dans la santé génétique d'une population. La mise en oeuvre d'un plan de conservation doit être proactive pour assurer le maintien de la qualité des unités opérationnelles de conservation. Les pêches commerciales et récréatives doivent être limitées; à cet égard, on examine plusieurs études de cas. On traite de l'importance d'éviter l'introduction d'espèces exotiques et de minimiser l'impact de la méthode d'échantillonnage, de même que des problèmes liés à l'ensemencement au moyen d'oeufs, d'alevins ou de tacons. Enfin, il est essentiel de sensibiliser le public à la valeur de la conservation de façon à ce que puisse être appliquée la pression politique nécessaire à la préservation des ressources naturelles.

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Introduction

Atlantic salmon (*Salmo salar*) conservation is inherently difficult due to the spatial and temporal complexity of the species' life history. Atlantic salmon migrate across freshwater, estuarine, and marine domains, freely crossing political boundaries within and outside their country of origin. They become the subject of land management issues, river resource usage, and allocation between competing fishing interests. Rearing habitats where salmon spawn and the young develop are often fragile habitats affected by pollution, forestry practices, and agriculture. In the marine environment salmon can undertake migrations that span most of the North Atlantic. They are frequently utilized in mixed stock fisheries, so nations must cooperate on harvest policies to ensure sufficient spawners return home. As such, conservation plans for Atlantic salmon are rarely developed by a single management entity, although some state agencies and river boards may develop their own plans. Putting cooperative plans in place is a daunting task, but there are a number of principals and important research areas that may be useful to consider in the making of these plans. This paper presents the results of the deliberation of a workshop panel formed to address the problems in developing a conservation plan for Atlantic salmon.

The panel recognized that the development of a conservation plan is a complex task that would require a broader cross-section of expertise than present on the panel. The panel also realized the investment required, in both time and resources, to learn the skills necessary to construct such plans. However, drawing upon the diverse expertise of the panel members, a number of ideas were developed which may be constructive for those interested in developing conservation plans for Atlantic salmon. This paper examines two general areas: the development and content of goal statements for conservation plans and the general framework for the implementation of a conservation plan. The elements under these subheadings are not intended to be a complete list, but rather, a collection of ideas and recommendations that planners might find useful.

Definitions

Four important terms related to conservation biology are defined according to Bradshaw (1996) and Fowler and Fowler (1971):

Restoration. The act of restoring to a former state or position, where the implication is of returning to an original state, one that is perfect and healthy.

Rehabilitation. The action of restoring to a previous condition or status. The term is similar to restoration except that there is no implication of perfection and no expectation of achieving the original state.

Enhancement. To raise or increase in price, value, importance or attractiveness.

Conservation. To maintain, protect, preserve or prevent from deterioration.

Rehabilitation and restoration incorporate the notions of time and change and have as an ultimate goal the recreation of some past condition. Thus, their reference point or target is sometime in the past. Enhancement implies improvement over the present situation. It may or may not take the original situation as the reference point. When enhancement seeks to improve by recreating past (supposedly better) conditions we are talking about restoration and rehabilitation (R&R) Thus, R&R is a particular subset of enhancement measures. However, enhancement may also consist in taking actions not necessarily aimed at restoring previous conditions. For example, the removal of a natural obstacle or the vaccination of fish against a natural disease are clearly not part of restoration and rehabilitation. Thus the reference (target) point of enhancement is either the past (R&R) or the future.

Conservation, protection, and preservation are synonymous terms. For clarity we will use the terms protection and preservation (P&P for short) and reserve conservation for the more general meaning of any plan aimed at maintaining ecosystems. Unlike R&R and enhancement, P&P does not aim to bring back past conditions, nor does it aim to create a future (hopefully better) state of affairs. P&P seeks to keep things the way they are, preventing further degradation, and thus anticipating future change. The reference point of P&P is the present. Thus, although all conservation plans are obviously projected into the future and have in common the notion of change, their target goals and scopes differ. In R&R, it is the past that is used as reference, in P&P it is the present, and in true enhancement it is the future.

Conservation goals

Adopting a unit of conservation

A critical issue in any conservation plan is to decide what to conserve. Some people might suggest that a conservation plan should save the species. However, we do not believe that the species is the appropriate conservation unit in the case of Atlantic salmon. First of all, the species is not threatened with extinction. In fact, there may be more Atlantic salmon alive than ever in history. The aquaculture industry alone produces over a hundred million Atlantic salmon, perhaps several times more than ever produced by nature (Gross 1998). Moreover, wild populations with many hundreds and thousands of free-swimming individuals can be found in at least some countries (e.g., Canada, Norway). Thus, the Atlantic salmon is not threatened as a species.

Instead, we suggest that a conservation plan must recognize that the Atlantic salmon species is composed of many evolutionary lineages whose survival is the issue for conservation. Because adult salmon migrate back to their natal spawning area and because these areas and migratory pathways may exert unique forces of natural selection, the Atlantic salmon gene pool has diversified into locally adapted units. The species is therefore a collection of unique populations with specialized adaptations (National Marine Fisheries Service 1995). These adaptations allow for viability within different stream habitats and may account for the broad geographic range occupied by the Atlantic salmon. Many of these populations are already extinct (e.g., much of the U.S.A. distribution) and others are vulnerable, threatened, or endangered. As the component parts are lost, so too is the species and its genetic heritage, part by part. Thus, the objective of a conservation plan for Atlantic salmon is to conserve its independent evolutionary lineages.

The Evolutionarily Significant Unit (ESU)

From a biological perspective the appropriate conservation unit for Atlantic salmon is the Evolutionarily Significant Unit (ESU). Waples (1991, 1995) defines an ESU as a "population (or group of populations) that (1) is substantially reproductively isolated from other conspecific population units, and (2) represents an important component in the evolutionary legacy of the species." The concept thus incorporates both the genetic and ecological diversity of the species. Although the ESU concept was originally developed for Pacific salmon, it has been found to be appropriate for the biology of Atlantic salmon as well (National Marine Fisheries Service 1995). It also has the advantage of official recognition within the US Endangered Species Act (National Marine Fisheries Service 1991; US Fish and Wildlife Service 1996), probably Canada's developing act (Bill C-65), and perhaps other countries with conservation acts that recognize distinct populations (e.g., Spain). Thus, the ESU meets the need to conserve the component parts of Atlantic salmon and may also allow access to legislation that could ensure immediate conservation action.

Applying the ESU

Methods for identifying ESUs are described in Waples (1991, 1995) and the papers in Nielsen (1995). In brief, genetic and phenotypic data (morphology, physiology, behaviour, life history (egg size, age of maturity, etc.) are collected, where logistically feasible, from populations throughout the Atlantic salmon range. These data are analyzed by phenetic and preferably cladistic methods and the relationship(s) among populations are determined by hierarchical nesting (Vogler and DeSalle 1994). Populations that do not differ significantly from each other are grouped into a single ESU. Each ESU becomes a biologically-determined unit for conservation (Fig. 1).

Limitations of the ESU

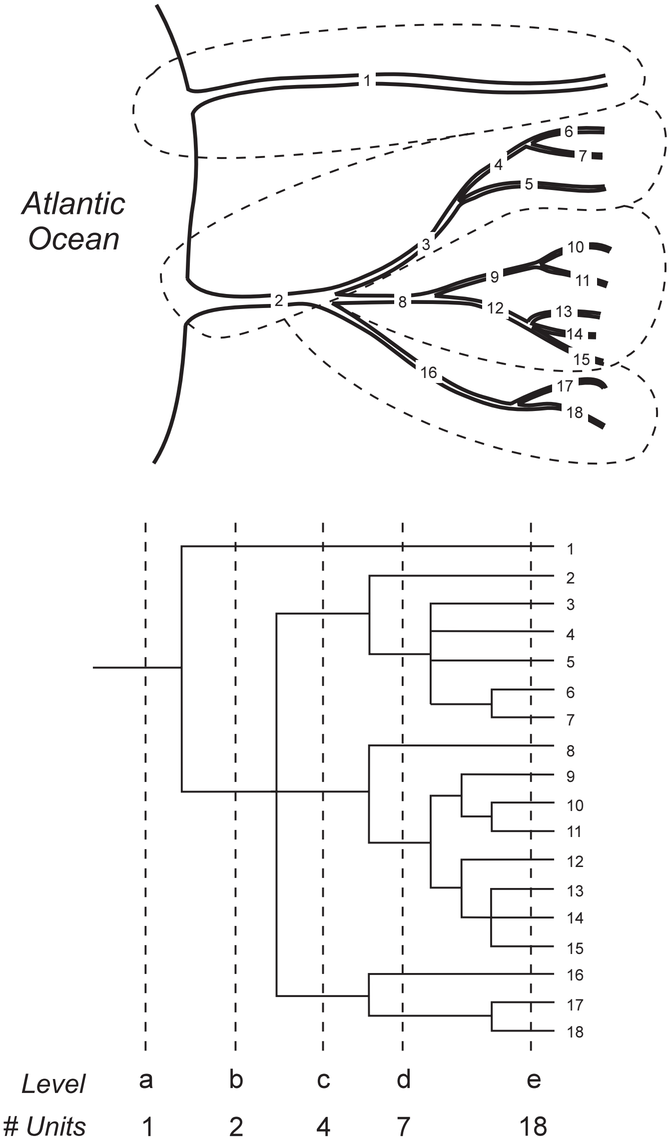
There is some controversy over the use of the ESU concept in conservation biology (see papers in Nielsen 1995). For example, there is no standard amount of significant difference among populations that is necessary to identify ESUs. As discussed by Waples (1995), a professional opinion must be applied in each case to the degree of difference that is deemed biologically significant.

Second, protecting ESUs is a "bottom-up" approach to conservation (Gross 1997). It identifies genetic and possibly ecological distinctions and ensures the protection of these. An alternative or "top-down" approach to conservation would place priority on preserving the ecosystem and assume that preservation of the ecosystem would also preserve the significant components of species. Waples (1995) points out that in order to preserve the ESU one must preserve the habitat on which it depends, thus by focusing on a definable unit one can work back up to the ecosystem.

Third, it is possible that not all distinctions between populations can be recognized by current measurement techniques. This would result in the grouping of populations of different lineages into a single ESU. Such grouping could result in the loss of the distinctions.

We recommend that the ESU be applied because it most clearly and effectively results in the preservation of genetic adaptations and the population structure required to maintain genetic diversity and the ongoing evolutionary process. In this way, the adaptations which allow survival in the present and the capacity for future adaptation through evolution are preserved for the Atlantic salmon.

Fig. 1. The two steps in identifying ESUs (adapted from Waples 1995: 24). First, one or more types of data are used to estimate evolutionary relationships among populations, as depicted here in a schematic diagram (top) and a phylogenetic tree (bottom). Second, a decision must be made regarding the appropriate hierarchical level on which to focus conservation efforts. For instance, a decision may be made to treat all 18 populations as conservation units (level e), or to recognize 7 units (level d), or 4 units (level c), or only 1 unit (level a). Here the decision is made to recognize 4 ESUs (distribution illustrated by dotted lines in upper panel). As all levels are consistent with the biological data, the final choice of hierarchical level may be influenced by social, economic and legal considerations. As such, the ESU becomes an Operational Conservation Unit (OCU).



Socio-economic issues

Decisions about conservation will rarely be based solely on biological information. Social, ethical, legal, and economic issues will also determine the conservation effort. In many cultures, people are willing to place only a certain economic value on conservation while in others the economic resources simply do not exist for conservation (Loomis and White 1996; Moyle and Moyle 1995). Since the goal of most human-based conservation of biodiversity is to ensure resources for humans, social, ethical, legal, and economic issues (summarized for simplicity as socio-economic issues) will play a major role in deciding the operational conservation unit (OCU).

Operational conservation unit (OCU)

The OCU is the unit of conservation that results from the interplay between biological requirements and socio-economic issues. The biological requirements are largely found within the ESU. The OCU therefore reflects the ESU and its interaction with socio-economic issues. In some cases, sufficient economic resources and desire may exist within society to preserve all ESUs and thus the ESUs become the OCUs. In most cases, however, the OCUs may be larger units than individual ESUs, encompassing several ESUs into a single OCU. This may lead to the loss of biological capacity of the species, although this loss is presumably balanced by the needs of society. Thus, decisions about the OCU must weigh the socio-economic and biological trade-offs.

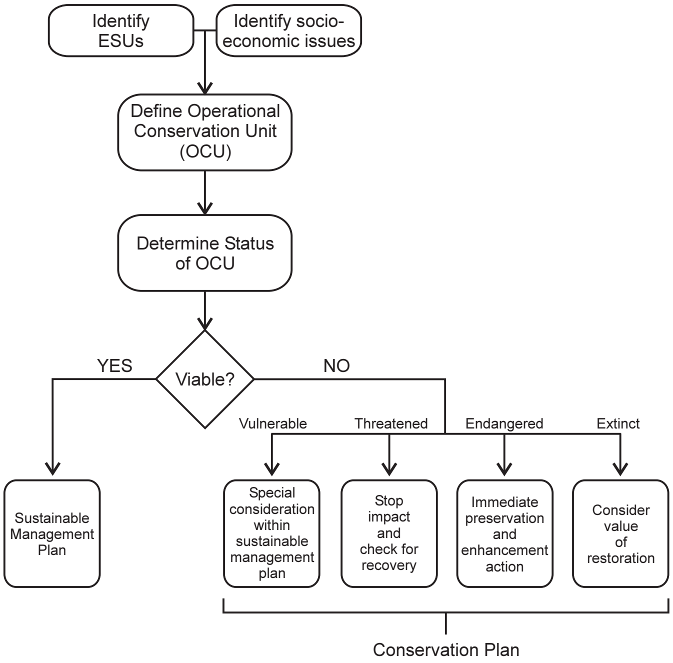
Applying the OCU

Developing a conservation plan for Atlantic salmon necessarily involves a series of stages. The first stage is to define the OCU. This is done through the identification of ESUs and socio-economic issues; through their mutual assessment by scientists, managers, and the public, a decision is made about the level of conservation (Fig. 2, and see below).

The second stage is to assess the status of the OCU (Fig. 2). Is it viable or not? Viability is determined through the genetic and ecological state of the OCU (see below), and also the existence of threats from human or other external activity to its habitat or individuals. For instance, the construction of a new pulp and paper mill within the ecosystem presents a habitat threat which must be taken into account in the assessment of the viability of the OCU.

If the OCU is found to be viable, a sustainable management plan is developed. This plan will allow harvesting without impacting the viability of the OCU. The management plan should be developed following the practices of “adaptive management” philosophy in which repeated trials are made under carefully observed conditions (Lichatowich et al. 1995). If the OCU is found not to be viable, it may be classified into one of several categories including vulnerable, threatened, endangered, or extinct, and an appropriate conservation action taken (Fig. 2). If vulnerable, the OCU should receive special consideration within a sustainable management plan. If threatened, current impacts should be immediately halted and the OCU checked for recovery. If endangered, immediate preservation and enhancement action is needed. Finally, if the OCU is extinct, then the value of restoration may be considered.

Fig. 2. The Operational Conservation Unit (OCU). The OCU is defined through the identification of ESUs and socio-economic issues. Viability is next determined through the genetic and ecological state of the OCU and also the existence of threats. If the OCU is found to be viable, a sustainable management plan is developed. This plan will allow harvesting without impacting the viability of the OCU. Alternately, the OCU may be found not to be viable. If classified vulnerable, the OCU should receive special consideration within a sustainable management plan. If threatened, current impacts should be immediately halted and the OCU checked for recovery. If endangered, immediate preservation and enhancement action is needed. If the OCU is extinct, then the value of restoration may be considered (from M. Gross, in preparation.)



OCUs and legislative boundaries

Protecting OCUs composed of stocks that migrate across boundaries to waters where they may be exploited or otherwise negatively affected without being legally recognized poses a problem to conserving a migratory species such as Atlantic salmon. The North Atlantic Salmon Conservation Organization (NASCO) is in the best position to implement policies on the protection of OCUs among its member states. NASCO’s convention applies to the salmon stocks which migrate beyond areas of fisheries jurisdiction of the coastal states of the North Atlantic north of 36° latitude throughout their migratory range. Stocks that migrate through the waters of adjacent states would require specific protection under the fisheries jurisdiction of neighboring coastal states. Since the council of NASCO establishes working arrangements with the International Council for the Exploration of the Sea (ICES) and other appropriate fisheries and scientific organizations, NASCO is seemingly the appropriate organization to insure the protection of OCUs across legislative boundaries.

Defining the value of the resource

The planning and application of a conservation plan is the result of perceived value associated with a resource (Riddell 1993; Scarnecchia 1988). Three values are defined that are commonly associated with a natural resource; biological, societal. and economic.

Biological value

This is the value associated with the unique genetic and ecological traits (adaptations) characterizing each ESU. Metapopulation structure that may involve several ESUs contributes to the maintenance of ecological stability and resilience as well as the evolutionary process. Conserving numerous ESUs allows life to continue in the face of future change. This is the value associated with the biological legacy of life on earth.

Societal value

This value is manifest in the desire to conserve in the absence of any monetary gain. Rather, the presence of the resource is associated with a sense of communal well-being or esthetic pleasure. For example, the traditional native American exploitation of some fish stocks whose importance in preserving a way of life through ceremony is far more valuable than the market worth of the fish; the restoration of degraded habitat uniquely for its esthetic value in increasingly urban environments; the conservation of nature for the purpose of retreat and the sense of well-being associated with being in contact with nature (e.g., the Biophilia hypothesis, Wilson 1984).

Economic value

This represents the financial returns obtained by directly exploiting the resource as a fishery, either for sport or commercial profit, or for the more general purposes of tourism.

The absolute value and relative importance of each value will vary according to the interests of the proponents of the conservation plan. In most cases, there may be conflict among resource users over the relative importance of each value. Furthermore, these categories are not necessarily mutually exclusive. An economic value may be applied to the first two categories by calculating the cash value forgone by not exploiting the resource for direct financial gain; alternatively, the biological legacy of life on earth may best be considered as priceless. The relative importance of each value must be determined in order to set the socio-economic stage on which OCUs are defined.

The functional plan

Assessment

Inventory of Atlantic salmon rivers and identification of keystone habitats

There is a need for a multi-scale habitat inventory of the Atlantic salmon rivers of the world in order to know what their status is relative to conditions prior to any major intervention/disruption to fish passage or habitat caused by human activities. The state to be measured and compared over time is the salmon potential of the river based on physical and biological habitat characteristics. If no biological data are available, relationships between habitats, river geometry, and drainage areas could provide preliminary information. Greater precision would be possible if detailed habitat information was available for stretches of river where change has occurred. Such comparisons between present and past conditions could guide the development of conservation priorities, as well as future restoration or rehabilitation programs. For example, by summarizing key physical parameters of present and historic salmon-bearing rivers (Table 1), the inventory could identify which rivers or river reaches would be most promising as habitat for re-introduced stocks. Other tabulated features, such as proximity to native wild salmon stocks, current catchment land use, and general ecological health would also bear on the potential of a river for rehabilitation as salmon habitat (as ranked in the last column of Table 1). Existing data bases could contribute to this effort; for example, the salmon rivers inventory maintained by NASCO.

At the within-river scale, salmon-bearing capacities of rivers depend in part on "keystone" habitats (Fig. 3). Although Atlantic salmon use a wide variety of stream habitats, there are certain critical, or keystone, habitats that strongly influence populations, either positively or negatively, that are great in proportion to the habitat's area. In the case of post-spawning adult salmon (kelts) for example, winter refugia from the potential effects of ice scour and accumulation, or from low stream flow, are often limited and best secured near the confluence of tributaries and main channels, behind islands, and especially in backwater channels (Komadina-Douthwright et al. 1997). Similarly, groundwater discharge zones and seeps often serve as thermal refugia during periods of high temperature stress (>23°C). Despite their very small areas, they are extremely important to heat-stressed salmonids.

There are general geomorphological relationships among rivers and within catchments that may permit identification of keystone habitats. The functional habitats of benthic insects and fish are related to the hydraulic conditions created by natural channel forms, for example in riffles, runs, meander bends, and scour pools. In some cases the preferred habitats coincide with the most frequently occurring hydraulic forms, suggesting that fish have adapted their behaviour to the natural geometry and behaviour of rivers (Newbury 1995).

A final consideration for restoration or rehabilitation projects is that the quality of habitat needed for re-introduced populations may be higher than the historical quality of rivers when they supported large salmon populations. Such "hystereses" could arise because of subtle effects. For example, large groups of spawning Pacific salmon coarsen the bed surface, reducing the probability of scour mortality for their young. If small numbers of salmon remain within a river system, for example, the size of gravels permitting successful reproduction may be more narrowly constrained.

Assessing population viability

(a) Demographic and ecological factors. Six variables that may be used to assess the viability, or health, of salmon populations. Healthy salmon populations exhibit the following characteristics.

Abundance. Healthy salmon populations exhibit recruitment levels sufficient to occupy all available habitat.

Table 1. Habitat inventory of the Atlantic salmon rivers of the world. The inventory would summarize the present status of salmon rivers relative to their historic extent and condition. The difference between past and present state provides a measure of the scarcity of salmon habitat (percentage habitat remaining, for example). At a finer scale, variables such as the number and kind of keystone habitats, water quality, current catchment land use, stock status (ecological and genetic viability) and the proximity to native wild salmon stocks as a source of colonists would also bear on the potential of a river for rehabilitation as salmon habitat. An index of restoration potential could be developed from some combination of these variables.

Country/ river	Historical state	Present state	Scarcity	Keystone habitats	Water quality	Land use	Stock status	Proximity to source	Restoration potential
Country 1									
River 1									
River 2, etc.									
Country 2									
River 1									
River 2, etc.									
Etc.									

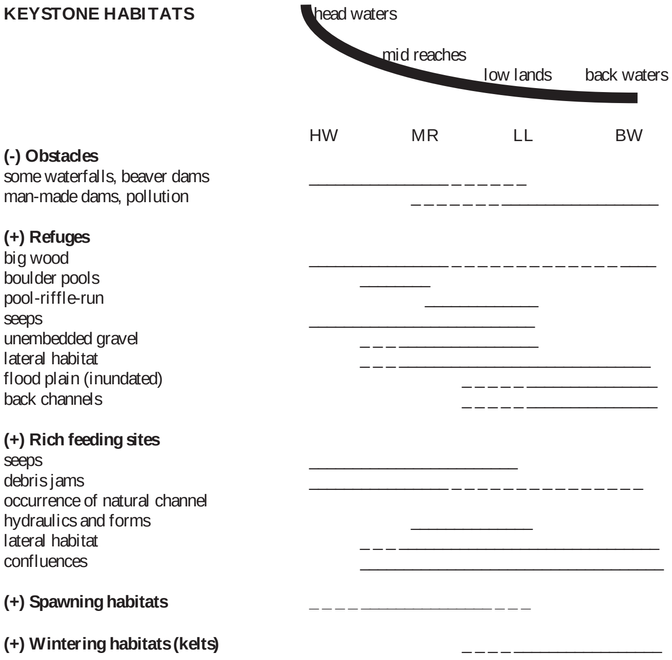


Fig. 3. Keystone habitats and their longitudinal distributions along drainage networks. Keystone habitats are grouped as obstacles, with negative effects on populations (–) and refuges, rich feeding sites and spawning habitats with positive effects on populations (+). HW, head waters; MR, mid reaches; LL, lowlands; BW, back waters.

Juvenile production is often maximal. The percentage habitat saturation (PHS; Grant 1998) is high, and fluctuations in population numbers are density-dependent. Self-thinning becomes the main regulatory factor controlling the size of the population, giving increased scope for intra-specific competition and selection.

Resilience. High resilience or the ability to recover from perturbations may be expected to characterize healthy populations. Resilience is favoured by rapid turnovers and high intrinsic rates of increase, and these will determine the ability to cope with stochastic demographic fluctuations.

Age and size structure. In healthy Atlantic salmon populations, all age classes are well represented and since age at maturity and age at migration to sea varies within the same population, there is variable, but significant, generation overlap that increases effective population size. Growth in size may be density-dependent, and stunted growth, if present, is often reversible.

Sex ratio. Factors that skew sex ratios of spawners in one direction reduce effective population size. Healthy populations will often show a variable but (on average) balanced sex ratio, roughly equal to 1:1.

Spatial distribution. Individuals within a healthy population occupy a heterogeneous environment at various spatial scales, from mesohabitats to different river reaches or tributaries. As a result the population has a high buffer capacity against exogenous disturbances, and the effect of catastrophic events is greatly reduced (risk partitioning).

Geographical distribution. Healthy populations are more likely to be found towards the center of their geographical range, where climatically-mediated habitat contractions are less likely to affect them. They are seldom isolated, and some straying from nearby streams assures a certain degree of gene flow.

(b) Genetic factors. A genetically viable population or ESU possesses genealogies that represent the evolutionary legacy of the species and the genetic variation upon which future evolutionary potential depends. The assessment of genetic viability should be directed at the monitoring and maintenance of the natural genetic diversity that reflects the local adaptation of the ESU in question. Artificial manipulation of genetic diversity and structure, or gene expression, through introductions or manipulation of the natural genetic architecture, do not serve the function of genetic health at the ESU level.

The power of genetic data rests in the large set of molecular characters generated through evolution that retain different temporal and spatial scales within the genome (allozymes, mtDNA, microsatellite loci, regulatory genes, gene expression). Assessments of genetic diversity need to use a suite of characters derived from the correct scale that portrays the historic and potential evolution of the species within its ESU. In any assessment, a clear knowledge of the assumptions imposed by the interpretation of patterns of genetic variation across the ESU landscape is important.

Four factors important to monitoring changes in genetic health within an ESU are identified.

Genetic diversity. Changes in genetic diversity are measured by shifts in the effective number of alleles per locus, frequency shifts in the most common allele, significant loss of rare alleles, analyses of genetic disequilibrium, and gametic disequilibrium (see Waples and Do (1994) for an explanation of terms). Temporal changes in allelic frequency in overlapping populations should be considered (Waples and Teel 1990). Analyses of changes in genetic diversity must take both genetic drift and natural changes in population structure within the ESU into account. Supplemental breeding programs frequently aim at increasing the size of a population without regard to the effects of genetic drift, which may be as important as inbreeding (Hedrick et al. 1995, Jorde and Ryman 1995). The introduction of supplemental stocks derived from fish populations from within the same ESU should be monitored for effects of genetic drift and inbreeding on locally adapted populations.

Effective population size. Monitoring the genetic viability of populations should include change in estimates of effective population size (N_e). N_e refers to an ideal population that is characterized by discrete generations, random mating, even sex ratios, where all individuals have the probability of contributing to the next generation (Waples 1990*a*,*b*). Obviously, this is not the case in wild salmonid populations. Distinctions should be made between inbreeding (N_{ei}) and variance (N_{ev}) effective numbers (Crow and Dennison 1988; Ryman 1994). There are several situations where these parameters can differ substantially based on whether a population is declining or increasing at the time of measurement (Waples and Do 1994; Ryman and Laikre 1991).

Genetic bottlenecks and founder effects. Patterns of genetic variability that document past or recent ecological and demographic events may serve as indicators of risk factors for genetic health of an ESU (Boyce 1992; Boileau et al. 1992; Lande 1993). Low levels of within- or between-population genetic variance within an ESU may indicate environmental catastrophes or anthropomorphic manipulations that have caused genetic bottlenecks and possible founder effects not detected by demographic or ecological surveys.

Reduction in population size followed by rapid growth creates conditions in which it is relatively easy for a population to shift from one co-dominant suite of genes to another (Slatkin 1996). In very small populations derived from much larger parent populations, genetic drift is the predominant factor, and it may overwhelm any selection differences among genotypes. In a rapidly growing population, after founder effect, genetic drift is relatively weak, even if the initial population is quite small, and selection will be most effective during and immediately after the period of rapid growth. Low-frequency alleles or co-adaptive complexes can be driven to fixation by selection (founder-flush) much more rapidly than they would be in populations of constant size (large or small; Slatkin 1996).

Gene flow. Natural populations tend to be subdivided to varying degrees by geographic and (or) physical barriers within their ESU that constrain movement and thus gene flow between certain populations (Rasmussen 1979; Selander 1970). Habitat choice and conspecific queuing in the context of patchy resources can result in the active aggregation of individuals with varying degrees of genetic relatedness (Barton 1995). The level of genetic differentiation and the effects of population subdivision on adaptive processes found within an ESU need direct documentation and extensive study to establish effective sampling regimes to monitor genetic health (Wade and McCauley 1988; Wade 1996).

Implementation

Anticipatory mechanisms and priorities

Protection of wild Atlantic salmon populations is a critical conservation goal. Past actions indicate that we are often in a reaction mode about addressing problems associated with salmon stocks and their habitats. Actions must be proactive to maintain the quality of the OCUs while focusing on foreseeable problems and predicting future threats. Incorporating protective measures for these anticipated events should also be considered.

Actions directed at the habitat for OCUs of Atlantic salmon should be focused on restoring and maintaining ecosystem processes that create and maintain habitats through time. It is important to insure that good habitats are identified and protected with consideration given to creating refuges in critical, keystone habitats. It is also important to maintain natural processes that account for changes to quality habitats and recognize that disturbance is an integral component of salmon OCUs in the future. It is important to educate salmon advocates and others that change is not necessarily negative. Salmon appear to be disturbance tolerant and may even require disturbance to some extent, an important subject for future research. Finally, it is important to consider the needs of other organisms in the development of a conservation plan for Atlantic salmon OCUs.

We suggest that the decision to protect an OCU considered to be in a healthy state is the first priority in a salmon conservation plan. Although the cost of such an action may be quite variable depending on context, such action may be considered low risk as the benefits in terms of biological, social, and economic values are high. Restoration and rehabilitation plans designed to recapture a previous state are more risky ventures. The cost of such work is high and the benefits in terms of social, biological, and economic values are difficult to evaluate. Finally, enhancement in order to create a new state is costly and inherently risky as the goal is, by definition, an unknown state. As funds for such conservation plans are limited, any specific plan must establish its own priorities.

Limiting commercial and recreational fisheries

Recreational and commercial catches are generally set with the intent of allowing the spawning escapement necessary to ensure future recruitment to maintain the stock. In Atlantic salmon, required spawning escapements should be related to the area available as spawning and rearing habitats, and their relative productivity. Survival and production and, therefore, the optimum spawning escapement may change in the system, either positively or negatively, due to any number of environmental variables. The Atlantic salmon is amenable to establishing stock-recruitment relationships for several reasons, including (1) stocks largely return to their natal river, (2) adults are not numerous and thus it is relatively easy to count them and evaluate key demographic characteristic (sex, age, weight), and (3) most of the individuals spawn once in their life. The relationship between stock and recruitment is generally modeled as a dome-shaped density-dependent relationship (e.g., Ricker 1954). Intraspecific density dependent mortality contributes to declines in survival above the optimum egg deposition (Gibson 1995). However, stock-recruitment relationships are at best noisy with density-independent variation, mainly resulting from the effects of river flows and temperatures or sea conditions, producing a wide scatter of points. As such, there is always a risk of missing management objectives by using deterministic functions describing the stock-recruitment relationship to set catch quotas.

Recently, the precautionary approach has gained acceptance as a basis for fishery management (Richards and Maguire 1998). The magnitudes of the uncertainties in fisheries management provide the principal justification for the precautionary approach. Resource managers must be advised in a way that portrays the potential consequences, or risks, of this uncertainty. In the words of Richards and Maguire (1998), an extreme interpretation of the precautionary approach could be management to such low risk that most fisheries would be closed. Conversely, management to a very high risk could lead to overexploitation at least to the point of economic extinction. The concept of the precautionary approach is included in a recent UN document of particular importance to the management of Atlantic salmon; the Straddling Fish Stocks and Highly Migratory Fish Stocks Agreement (UN 1995). Unfortunately, the number of countries ratifying the agreement is not sufficient for it to be incorporated into the Law of the Sea (Richards and Maguire 1998).

The precautionary approach appears to be the best approach to the management of Atlantic salmon stocks. The situation is serious enough that the commercial exploitation of Atlantic salmon at sea is being managed to such low risk that many interceptory fisheries are being closed or strongly curtailed. For example, in May of 1998, the Quebec provincial and Canadian federal governments announced a voluntary buy-back program aimed at eliminating the 87 Atlantic salmon fishing licenses along the north shore of the Gulf of St. Lawrence east of Natashquan, thus effectively ending commercial fishing in Québec waters. Also in 1998, the Canadian government announced a moratorium on the commercial salmon fishery in northern Labrador. In 1997, there were 205 licensed commercial salmon fishermen in northern Labrador who captured 47 t against a total quota of 50 t. Finally, the West Greenland fishery quota was reduced from 57 to 20 t in 1998.

Marine commercial fishing continues in the Northeast Atlantic. For example, in 1997, Ireland reported commercial catches of 570 t, Norway, 630 t, and the United Kingdom (England and Wales), 103 t. Current catch levels are markedly lower than in the recent past, with the 1997 catch of all homewater fisheries in the Northeast Atlantic (except Northern Ireland) below both the 1992–96 and 1987–96 means (Anonymous 1998*a*). This is believed to reflect both reductions in fishing effort and reductions in stocks. Some marine fisheries could conservatively be conducted where they can be exploited on known river stocks close to home rivers and sufficient escapement allowed for spawning and angling.

Hook-and-release angling has become a major conservation measure. In Newfoundland and the three Canadian maritime provinces, it has been mandatory to release all salmon >63 cm fork length (FL) (considered as salmon having passed 2 or more winters at sea) hooked by anglers since 1984. In New Brunswick, there is unlimited hook-and-release of kelts (salmon migrating to sea following their post-spawning, over-winter residence in freshwater) provided the angler has not taken the daily bag limit of 2 small salmon. After May 15, anglers may hook-and-release 4 salmon per day if they have not exceeded their small-salmon bag limit.

In Newfoundland and Labrador, the precautionary approach is well illustrated by the establishment of in-season reviews in 1998 to determine management directives. Prior to the July in-season review, anglers are allowed to retain only one small salmon (<63 cm FL). The Department of Fisheries and Oceans uses a traffic-light analogy to express its decisions following the in-season reviews; green light: if the in-season review indicates that returns are above or at the level of the average annual returns for the period 1992–1996, anglers would be able to retain three additional small salmon. Amber light: if the review indicates that returns are between the average annual returns for the period 1992–1996 and the poor returns observed in 1997, the single small salmon retention limit would remain in effect for the remainder of the season. Red light: if the review indicates that returns are below those observed in 1997, retention would be prohibited for the rest of the season. Hook-and-release fishing is permitted only if water temperatures do not exceed 18°C to prevent the increased mortality that occurs above this temperature (stock assessments assume 10% mortality of hooked-and-released salmon). For rivers given the green or amber light, all angling is stopped if the water temperatures exceed 22°C.

In Québec, each of its 118 salmon rivers will fall under a new, precautionary, management scheme beginning in the year 2000. The approach uses the stock-recruitment model of Schnute and Kronlund (1996) based on a parameter that determines the type of stock-recruitment curve and two management parameters: the maximum sustainable catch and harvest rate. Because of the uncertainty surrounding key population and policy parameters, the Bayes posterior probability distribution (Walters and Ludwig 1994) is applied to key parameters in order to calculate the risks of alternative management decisions to the conservation of the resource and the maintenance of local resource exploitation (Dr. P.-M. Fontaine, Fédération Québecoise pour le Saumon Atlantique, personal communication).

Finally, there is considerable discussion and controversy over the question of predator control as a means of increasing Atlantic salmon production and spawning escapement. There are 6 seal species that are considered as potential predators of salmon in eastern Canada (harp, hooded, ringed, bearded, harbor, and gray) (Anonymous 1998*b*). Although very few salmon were found in the stomachs of about 10 000 seals examined, seals may nevertheless represent an important source of mortality given the inverse abundance of seals and Atlantic salmon. This potential source of mortality may be more important in or near river mouths, but appropriate studies have not yet been conducted to test this hypothesis. In addition, cormorants, mergansers, and kingfishers have diverse diets, including Atlantic salmon, that reflect the broad range of species found in their habitats. Smolts appear particularly vulnerable; the diets of double-crested cormorants from all regions of Atlantic Canada combined was 17.3% Atlantic salmon during smolt runs but only 0.1% at other times of the year (Cairns 1998). The author cautions that the data are strongly biased by differential digestion rates, incomplete spatial and temporal coverage, and an over-representation of samples from salmon rivers. It appears that well-controlled experiments need to be conducted to conclusively demonstrate that predator-control programs do in fact improve salmon runs. However, the control of populations of predatory species (particularly seals) as part of a management plan to conserve Atlantic salmon is fraught with ethical problems and would surely meet with resistance from many sectors of society.

Exotics

The preservation goal of a conservation plan implies the maintenance of natural conditions within the local environment that are important to the survival of the target species (Nelson and Soulé 1987). Changes in inter- and intraspecific competition, levels of predation, and the introduction of novel diseases that occur when exotics are introduced into an ESU conflict with this goal. Exotics include introduced species, conspecific introductions from geographically and genetically divergent ESUs (see Nielsen 1994), and transgenic individuals. The natural state of ecological balance within an ESU may shift with introductions, producing subsequent shifts in the evolutionary potential of the species. All introductions must be judged on their potential impact on the evolutionary dynamics of the ESU.

Purposeful introductions of new species or conspecifics from other ESUs must be avoided. Conspecific introductions or transplantations within an ESU must fit the evolutionary strategies of the species and respect the genetic integrity of the ESU. Unintentional introductions must be eliminated as soon after discovery as possible.

Minimizing the impact of sampling methodology

Many standard methods of collecting data may have negative effects on the salmon populations we study. There is some evidence that the population of salmon under study has declined after counting fences were installed (e.g., Murray 1968). Although adult trapping facilities are valuable in long-term studies (e.g., Kennedy and Crozier 1993), less damaging methodologies should be considered where possible, such as redd counts, mark-recapture, catch-per-unit-effort in the commercial and angling fisheries and underwater observations. Handling should be curtailed by using less stressful techniques such as electronic, acoustic, or video counters. Where adults must be handled for tagging or tissue sampling, capture is best undertaken some distance upstream so that fish have had a few days in freshwater and the epidermis is thicker. Smolts are more fragile than parr and survival may be decreased by handling (Saunders and Allen 1967).

Electrofishing is effective in capturing young salmon in riffle habitats; if the proportion of catch is high, estimates by the depletion method are possible (Bohlin et al. 1989). However, the long-term effect of electrofishing on fish and invertebrates requires study. In systems where young salmon are distributed in a wider range of habitats, such as pools and lakes, electrofishing is less effective. In these habitats population estimates are better made by mark and recapture methods. A number of methods can be used to capture fish in these habitats, such as beach seine, fyke nets, trap nets, or purse seine. Where eels are abundant fyke or trap nets should not be used, since predation on the parr can be high in the traps (Gibson et al. 1987). Angling with small flies can be used to capture in situations where other methods are difficult to use (Gibson 1973), but efficiency depends very much on the skill of the angler and fry are poorly represented.

The technique of direct observation of young salmon by diving was first used by Keenleyside (1962) and is now a common method for observing behaviour and habitat use (e.g., Heggenes and Saltveit 1996). Although useful as an index, the technique may not provide accurate population estimates (Cunjak et al. 1988). Video technology is being used to extend the range of underwater observation.

Power (1993) has pointed out that the traditional method of obtaining data on diet and food consumption by wild fish is not acceptable, since it involves killing too many fish. He suggests that a physiological approach should be used to evaluate energy needs of Atlantic salmon parr in relation to temperature, growth, competition, and the food required to support production. Stomach flushing can be used to identify gut contents without sacrificing fish.

Enhancement pitfalls

The most common enhancement procedure is the supplementation of the stocks by the planting of eggs, or fry, or the release of older stages. Fry may be released unfed, shortly after “swim up,” or as fed fry at some time later in the season. Young salmon may be released as parr, or “fingerlings,” or they may be released as smolt, the stage at which they migrate to sea. Hatcheries are required for most of these procedures. A major problem associated with hatchery rearing is that relatively few genotypes are selected so that the genetic variability found in the natural population is not present. Another major problem is the extensive artificial selection that occurs in the hatchery environment, favouring genes that are different from those favoured by nature (Fleming and Gross 1993; Fleming et al. 1994). If fish are reared to older stages, a proportion of the young salmon die, further selecting for fish that would be less fit for natural conditions. A third problem is the direct effect on development of the phenotype (Fleming et al. 1994, 1996). To overcome some of these difficulties in rearing, the hatchery may develop a brood stock that provides progeny suitable for hatchery rearing. However, since these fish have even less genetic diversity and are more strongly under artificial selection, they are even less likely to survive in the wild. Behavioural differences between hatchery and wild salmon parr reduce their ability to survive once released (Dickson and

MacCrimmon 1982). Furthermore, fish may be released at an inappropriate time, when suitable prey items are not available, or they may compete with and have negative effects on naturally produced fish, because the hatchery fish are bigger or more aggressive, or through competition for food or habitat. There is evidence that native salmon have been negatively affected by “enhancement” with stocking of non-native stock, which may have lacked some adaptation for the receiving river. In Newfoundland some rivers with supposedly low runs are “enhanced” by capturing wild salmon from the same river and the progeny are artificially reared so that they can be released upriver the following year. The reasoning is that survival through hatching is greater in the hatchery than in the river. However, follow-up studies must be undertaken to measure survival success of the stocked fry relative to wild fry as it is possible that no beneficial effects result. Stocking hatchery fish, or preferably introducing wild salmon, may be beneficial in the restoration of rivers that have lost their original stock.

Enhancement frequently involves opening up previously inaccessible parts of a watershed, by removing obstacles or providing fishways around the obstacle. A possible problem associated with this practice is that the fish community above the previously inaccessible barrier is likely to be changed when anadromous salmon colonize the river. In some cases species other than salmon may also be allowed access. Such waters in Newfoundland, for example, frequently have endemic populations of brook trout, landlocked salmon, and arctic char. Economically, anadromous salmon may be preferred, but biologically this could be less desirable if the endemic species are negatively affected. In addition, invertebrate and amphibian populations that require fishless habitat may be exterminated by this practice.

Enhancement may involve fertilization of lakes or streams. Oligotrophic conditions are therefore likely to become more eutrophic. This can be beneficial to increase production of young salmon (Gibson and Haedrich 1988), especially in regions where there is a depauperate fish fauna, so that competing species would not be enhanced. However, the plant and invertebrate communities are changed, so that although fish production is increased, the stream may no longer be regarded as “healthy.”

Communication

If human activities are to be sustainable, we need to ensure that the ecological systems on which our economies depend are resilient. Arrow et al. (1996) recommend institutional reforms that would compel private users of environmental resources to take account of the social costs of their actions. The problem involved in devising environmental policies is to ensure that resilience is maintained, even though the limits on the nature and scale of economic activities thus required are necessarily uncertain. They emphasise the need for reforms that would improve the signals that are received by resource users. Harte (1996) assesses the two generally held views of future development, one of which is that nature is the ward of humanity and the other that it is the steward. He believes that the common sense values underlying the nature-is-steward vision are not being communicated adequately to the public. He claims that we are losing the educational battle because the science underlying the nature-is-steward vision does not appear to be as convincing, let alone as dazzling, as is the science underlying the people-are-stewards vision of continuing growth and of conversion of wild habitat to manacled rivers and manicured forests. It is in the global interest to keep as much biodiversity as possible at the genetic, species, and ecosystems levels (Fuentes-Quezada 1996).

Although loss and degradation of habitats, and harvesting, are acknowledged to be the major negative factors that have caused the demise or decline of salmon stocks, enforcement of regulations is weakly applied unless there is “political will” or, in other words, public awareness and public political pressure. A relatively minor example of the advantages of public interest, but repeated in other areas in the last decade, could be the city rivers of St. John’s, Newfoundland. Up to 15 years ago fisheries regulations concerning habitat were consistently ignored, wetlands were filled in, streams channelized or put underground, riparian vegetation removed for developments, and storm sewers, with added effluents, discharged directly into streams (Gibson and Haedrich 1988; Steele et al. 1993). Environmental groups then fought to control the destruction and with political pressures ensured that habitat regulations were enforced, and enhancement programmes have followed. After several years of government lobbying, a local group received permission to stock salmon as fry, which are thriving and salmon runs are likely to be restored. The example has encouraged other municipalities on the island to follow suit. The environmental movement concomitant with public education on the values of habitats has slowed loss of habitats across the country, and improved waters in some areas.

In discussing the philosophy of ecosystem management and the necessity of public education and communication, Schramm and Hubert (1996) suggest that the concepts of optimum sustained yield and ecosystem management are similar. Ecosystem management involves changing the spatial and temporal scales of management from a focus on the local scale and immediate benefits to broader geographical scales (the entire watershed and beyond) and long-term benefits. There must be a collaborative approach involving a diverse array of stakeholders. Communication among resource managers and their agencies is necessary. Communication within agencies is necessary, and managers and field staff must understand the philosophy, how to implement it, and how to communicate with and raise input from the public.

The research conducted to develop our understanding of salmon ecology must also be communicated to the general public to foster public awareness of the value of conservation. Public lectures, articles in the popular press, public involvement in research projects and general visibility of scientific research are all means to heighten public understanding of natural ecosystems. Such understanding is essential if the public is to be expected to support the biological and societal values of nature, rather than economic exploitation, and apply the political pressure necessary to preserve natural resources.

Research strategies

To fill the gaps in our knowledge about Atlantic salmon and their habitats and to implement meaningful conservation plans, we should consider changing the way we do research.

In particular, we must develop networks of multidisciplinary and international research groups working together on common goals. Collaboration among university, government, and industry to set up such networks is essential, permitting access to public research funds that are increasingly targeted to such efforts. Furthermore, such networks are important tools for advocacy, providing the visibility and impact necessary to influence public opinion and hence, government policy. Although the efforts of individual research laboratories remain the backbone of the scientific enterprise in most countries, collaboration offers the promise of significant advances in knowledge beyond the reach of individual laboratories.

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