INTRODUCTION / INTRODUCTION

The status of Atlantic salmon (*Salmo salar*): populations and habitats

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Abstract: The important decline of Atlantic salmon (*Salmo salar*) across its range during the past three decades, despite numerous management and conservation programmes, is an alarming index of the vulnerability of this species. The following series of papers was produced to summarize current knowledge on specific interactions between biotic and abiotic variables that may contribute to determine the survival of Atlantic salmon. Evaluation of the challenges encountered in spawning grounds (siltation, oxygenation), nursery habitats (substrate, trophic interactions), overwintering habitats (flow conditions, winter feeding opportunities), and coastal and oceanic environments (water temperature, predators, parasites) suggest that all habitats required by Atlantic salmon and all processes that occur in each habitat represent a critical link that allows this species to persist. Management practices employed during artificial fish selection, incubation, and stocking also affect the success of restoration efforts. Because limiting factors may change in time and because our ability to intervene in specific habitats may be minimal, the only strategy within our reach may be to continue gathering information about processes that determine the fragility of Atlantic salmon and, in the light of our findings, to implement scientifically sound actions where and when possible.

Résumé : L'important déclin du saumon atlantique (*Salmo salar*) sur toute son aire de distribution au cours des trois dernières décennies, malgré de nombreux programmes de gestion et de conservation, est un indice alarmant de la vulnérabilité de cette espèce. La présente série d'articles a été produite pour résumer les connaissances actuelles au sujet d'interactions spécifiques entre des variables biotiques et abiotiques qui peuvent contribuer à déterminer la survie du saumon atlantique. L'évaluation des défis rencontrés sur les sites de fraie (siltation, oxygénation), dans les habitats nourriciers (substrat, interactions trophiques), dans les habitats d'hivernage (condition du courant, opportunités d'alimentation hivernale) et dans les environnements côtiers et océaniques (température de l'eau, prédateurs, parasites) suggèrent que tous les habitats requis par le saumon atlantique et tous les processus qui s'effectuent dans chaque habitat représentent des maillons critiques qui permettent à cette espèce de persister. Les pratiques de gestion employées durant la sélection artificielle des poissons, l'incubation, et l'introduction affectent aussi le succès des programmes de restauration. Parce que les facteurs limitants peuvent changer dans le temps et parce que notre capacité à intervenir dans certains habitats est limitée, la seule stratégie à notre portée est de continuer à accumuler des informations au sujet des processus qui déterminent la fragilité du saumon atlantique et, à la lumière de ces observations, enclencher des actions scientifiquement défendables où et quand c'est possible.

Introduction

Everything about Atlantic salmon (*Salmo salar*) once inspired a sense of grandeur; the potential size of individuals, the number of fish that roamed the rivers and the seas, and the wide distribution of the species. These fish also evoked images of majestic and pristine rivers, quasi-mythic journeys to the ocean and back to their original birthplace, and an instinctive determination to persist in spite of numerous challenges. These attributes fully justified the cultural, social, and economic status held by this species. The decline of Atlantic salmon across its range during the past three decades, despite the international ban on commercial harvesting on ocean feeding grounds and the implementation of numerous conservation programmes in rivers, now compels us to acknowledge the fragility of this species. The follow-

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ing series of papers represent a glimpse of the current knowledge on the effect of interactions between biotic or abiotic variables on Atlantic salmon.

Egg survival and embryo development

The survival and development of Atlantic salmon is affected by numerous physical conditions even before hatching. Experiments performed by Lapointe et al. (2004) to assess the relationship among egg-to-emergence survival, substrate composition, and hydraulic conditions suggest that a few percent of silt in reeds may have a strong negative effect on egg-to-emergence survival. This study further indicates that the magnitude of the effect of silt may increase with the sand content of the substrate. One consequence of this finding is that the interstitial flow required to maintain egg-to-emergence survival may vary with the relative contribution of silt and sand to the substrate. In addition to substrate composition and flow conditions, the supply of oxygen necessary for egg survival and embryo development may also depend on hydrological features. Youngson et al. (2004) estimated the impact of oxygen-poor, long-residence ground water on the survival and development of Atlantic salmon embryos. Their field experiments indicate that low levels of hyporheic oxygen may have a negative effect on embryos' survival and size, particularly when incubation occurs deep in the substrate. This study therefore underlines the potential importance of assessing the effect of long-term hyporheic ground water on the production of Atlantic salmon in rivers. In addition, it was noted that eggs laid near the surface of the substrate may suffer from physical disturbances. This also provides a new insight on the dilemma faced by spawners regarding the depth in the substrate at which eggs should be laid to maximize egg-to-emergence survival.

Interactions between phenotypes and environmental conditions for fry and parr

Some approaches that are employed to avoid problems caused by the harsh conditions that may occur during the incubation period include the use of in situ incubators designed to minimize egg disturbance and the stocking of fry or parr in rivers. Laboratory and field experiments showed that the rearing conditions (hatchery or stream) and the timing of fry introduction to a river relative to (*i*) the emergence of other groups of fry, (*ii*) water temperature fluctuations, or (*iii*) flow regime have a marked influence on fish size and survival (Letcher et al. 2004). These interactions do not only influence the fry stage but persist through time and could be perceived in the size, survival, and expression of life-history traits in parrs. Such information may influence the current stocking practices and may improve the success of fry introduction as a means to support conservation and restoration efforts. Although the manner and timing of fry introduction may be important, matching fish phenotypic attributes with environmental conditions may also contribute to the success of stocking operations. There are relatively few examples of tests of the relative ecological or physiological performance of fish with different phenotypes. Enders et al. (2004) compared the swimming metabolism of three phenotypes of Atlantic salmon parrs (wild, farmed, and domesticated) from Canada and Norway. In contrast with traditional respirometry studies that use quasi-laminar flows in tube respirometers, the experimental flows tested were turbulent. This study shows that the physiological costs of swimming against a turbulent flow is 2.4- to 4.0-fold higher than predicted by models developed using quasi-laminar flows. While the swimming metabolism did not vary between wild and farmed parr, both were significantly lower than swimming metabolism of domesticated parr, indicating that artificial selection may have a negative effect on the ability of domesticated parr to cope with turbulent flows. Whether or not all wild populations conform to a single respiration model is presently difficult to establish, because relatively little is known about the magnitude of the phenotypic differences that may exist among a larger number of natural populations of Atlantic salmon. In this context, Obedzinski and Letcher (2004) performed a series of common environment experiments intended to assess among-population phenotypic differences attributable to genetic variations. They found that conclusions about the existence or magnitude of phenotypic differences among five populations of Atlantic salmon might vary with the life stage considered (i.e., egg, alevin, early parr, late parr). Their work clearly shows that the study of phenotypic variations and stock differentiation not only requires the examination of numerous traits but that traits should also be examined at numerous life stages. Yet the source of this variation remains unknown. Determination of the relative effect of adaptations to river-specific environments and hatchery selection on genetically based phenotypic differences requires the study of the environmental conditions experienced by fish in rivers.

Parr distribution patterns and their consequences

The relationship between fish and environmental conditions may be described using habitat preference indices. For instance, environmental conditions used by Atlantic salmon aged 0–5 years in a subarctic river were determined by estimating their preference for specific ranges of water depth, flow velocity, and substrate composition during the summer, autumn, midwinter, and late winter (Mäki-Petäys et al. 2004). This field study shows that habitat preferences may vary among seasons, particularly for older parr that tend to move from rapid to low-flow velocities during the winter and spring. This change in the distribution of older parr may also modify the interactions between fish of different age classes. This study indicates that the proper analysis of fish–habitat interactions in rivers calls for age- or size-specific descriptions of the seasonal variations of the physical conditions required by Atlantic salmon. Although it is important from a management perspective to identify the environmental conditions preferred by fish, it is also useful to assess the consequences of environmental conditions on correlates of fish fitness.

Environmental conditions and habitat selection are expected to have a direct impact on fish foraging, growth, and survival. Girard et al. (2004) examined this issue and found that in the summer, habitats preferred by 0+ fish provided superior access to food (higher drift of invertebrates) and higher foraging rates than habitats avoided by these fish. Their study also showed than fish size, growth, and survival do not vary among habitats assigned different preference indices. While higher fish densities in preferred habitats are consistent with the predictions of an ideal free distribution, comparisons with other studies suggest that Atlantic salmon may shift from an ideal free to an ideal despotic distribution, depending on fish densities and habitat types. Hence, the study of the energetic consequences of fish distribution in rivers may require that ideal free and ideal despotic schemes be taken as complementary instead of mutually exclusive hypotheses.

Interactions between environmental conditions and habitat selection in the winter are generally anticipated to affect parr survival. However, experiments to quantify the effect of flow velocity and shelter availability on parr revealed that variations of environmental conditions in winter may not only affect parr survival but also their ability to maintain a given size or, in some cases, to maintain and even increase their energy density (Parrish et al. 2004). Similarly, Finstad et al. (2004) found that as the winter progresses, 2+ and 3+ parrs with low energy densities may be selectively removed from natural systems because of an energy-dependent mortality. This study also indicates that parr overwintering mortality is defined by a critical energy density and not by fish size. These observations suggest that management operations aimed at increasing the availability of conditions that would allow parrs to feed during the winter may also allow them to maintain or increase their energy density and to improve their survival during this period.

Life in coastal and oceanic habitats

The conditions encountered by smolts as they exit their native rivers differ from their original environment in terms of water temperature, water salinity, prey, predators, and parasites. The differences between riverine and coastal habitats represent a series of environmental stressors to which smolts must rapidly adapt. However, as emphasized by the review in Jonsson and Jonsson (2004), both coastal and oceanic habitats changed over the past few decades. More specifically, features such as the size of a proper thermal habitat for growth in the ocean may have significantly decreased during this period. This reduction, which may be a consequence of global climate change, may affect growth and survival and key life-history traits such as fish size and age at maturity. Niemelä et al. (2004) supported this view by showing that during the period of 1972–2003, part of the variation in salmon catches for stocks that showed no consistent trend of decline could be related to mean sea temperature in July during the year of smoltification. Global climate change was also invoked by Juanes et al. (2004) to explain a shift in the timing of the upstream migration of adults from numerous North American stocks during the past 23 years. Although the exact mechanism by which this shift occurs is not completely understood (changes in river discharge, river temperature, oceanic temperature), the timing of upstream migrations may affect the environmental conditions experienced by fish in rivers and the survival of mature fish.

Spawners

From a population dynamics standpoint, the most important contribution of spawners is the production of fertilized eggs. In many systems, a significant fraction of the adult population of Atlantic salmon dies after spawning. Nislow et al. (2004) developed a framework designed to identify the life-history interactions that may determine whether Atlantic salmon migrations result in the net importation or the net exportation of nutrients for freshwater systems. This study suggests that the low numbers of adults currently returning to spawn may not have a negative effect only on the number of eggs deposited in rivers, but also on the general productivity of the nursery areas, and consequently, on the growth and survival of fry and parr.

Conclusion

The present series of papers provides new knowledge about the impacts of interactions between biotic and abiotic variables on Atlantic salmon throughout their life cycle. These papers illustrate that all habitats required by Atlantic salmon and all processes that occur in each habitat represent a link in a chain of events that allows this species to persist. The relative importance of elements that contribute to the fragility of Atlantic salmon is difficult to define because of (*i*) the diversity of habitats required by these fish to complete their life cycle, (*ii*) the complexity of the interactions between biotic or abiotic variables in these habitats, and (*iii*) the range of spatial and temporal scales at which these interactions operate. The identification of key determinants at this point in the history of the species may be conjectural and futile. Limiting factors may change in time, and our ability to intervene in specific habitats is sometimes minimal. Unfortunately for scientists, managers, and Atlantic salmon, the only strategy within our reach may be to continue gathering information about processes that determine the fragility of Atlantic salmon populations and, in the light of these findings, implement scientifically sound actions wherever and whenever possible.

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References

Enders, E.C., Boisclair, D., and Roy, A.G. 2004. The costs of habitat utilization of wild, farmed, and domesticated juvenile Atlantic salmon (*Salmo salar*). Can. J. Fish. Aquat. Sci. **61**: 2302–2313.

Finstad, A.G., Ugedal, O., Forseth, T., and Naesje, T.F. 2004. Energy-related juvenile winter mortality in a northern population of Atlantic salmon (*Salmo salar*). Can. J. Fish. Aquat. Sci. **61**: 2358–2368.

Girard, I.L., Grant, J.W.A., and Steingrímsson, S.Ó. 2004. Foraging, growth, and loss rate of young-of-the-year Atlantic salmon (*Salmon salar*) in relation to habitat use in Catamaran Brook, New Brunswick. Can. J. Fish. Aquat. Sci. **61**: 2339–2349.

Jonsson, B., and Jonsson, N. 2004. Factors affecting marine production of Atlantic salmon (*Salmo salar*). Can. J. Fish. Aquat. Sci. **61**: 2369–2383.

Juanes, F., Gephard, S., and Beland, K.F. 2004. Long-term changes in migration timing of adult Atlantic salmon (*Salmo salar*) at the southern edge of the species distribution. Can. J. Fish. Aquat. Sci. **61**: 2392–2400.

Lapointe, M.F., Bergeron, N.E., Bérubé, F, Pouliot, M-A., and Johnston, P. 2004. Interactive effects of substrate sand and silt contents, redd-scale hydraulic gradients, and interstitial velocities on egg-to-emergence survival of Atlantic salmon (*Salmo salar*). Can. J. Fish. Aquat. Sci. **61**: 2271–2277.

Letcher, B.H., Dubreuil, T., O'Donnell, M.J., Obedzinski, M. Griswold, K., and Nislow, K.H. 2004. Long-term consequences of variation in timing and manner of fry introduction on juvenile Atlantic salmon (*Salmo salar*) growth, survival, and life-history expression. Can. J. Fish. Aquat. Sci. **61**: 2288–2301.

Mäki-Petays, A., Erkinaro, J., Niemelä, E., Huusko, A., and Muotka, T. 2004. Spatial distribution of juvenile Atlantic salmon (*Salmo salar*) in a subarctic river: size-specific changes in a strongly seasonal environment. Can. J. Fish. Aquat. Sci. **61**: 2329–2338.

Niemelä, E., Erkinaro, J., Dempson, J.B., Julkunen, M., Svenning, M.A., Ingvaldsen, R., Holm, M., and Hassinen, E. 2004. Temporal synchrony and variation in abundance of Atlantic salmon (*Salmo salar*) in two subarctic Barents Sea rivers: influence of oceanic conditions. Can. J. Fish. Aquat. Sci. **61**: 2384–2391.

Nislow, K.H., Armstrong, J.D., and McKelvey, S. 2004. Phosphorus flux due to Atlantic salmon (*Salmo salar*) in an oligotrophic upland stream: effects of management and demography. Can. J. Fish. Aquat. Sci. **61**: 2401–2410.

Obedzinski, M., and Letcher, B.H. 2004. Variation in freshwater growth and development among five New England Atlantic salmon (*Salmo salar*) populations reared in a common environment. Can. J. Fish. Aquat. Sci. **61**: 2314–2328.

Parrish, D.L., Hawes, E.J., and Whalen, K.G. 2004. Winter growth and survival of juvenile Atlantic salmon (*Salmo salar*) in experimental raceways. Can. J. Fish. Aquat. Sci. **61**: 2350–2357.

Youngson, A.F., Thorley, J.L., Malcolm, I.A., Soulby, C., and Bacon, P.J. 2004. Long-residence groundwater effects on incubating salmonid eggs: low hyporheic oxygen impairs embryo development. Can. J. Fish. Aquat. Sci. **61**: 2278–2287.