# Juvenile production variation in salmonids: population dynamics, habitat, and the role of spatial relationships

## John F. Kocik and C. Paola Ferreri

**Abstract**: Anadromous Atlantic salmon (*Salmo salar*) exhibit a complex life history that requires the use of habitats that span several different temporal and spatial scales. While fisheries scientists have investigated the various elements of habitat and how they affect Atlantic salmon growth and survival, these studies typically focus on requisite requirements for a single life history stage. Current advances in our understanding of salmonid populations in lotic systems indicates that ignoring the spatial positioning of different habitats and dispersal capabilities of fish between them may affect estimates of habitat quality and production of juvenile Atlantic salmon. Using the concepts of juxtaposition and interspersion, we hypothesize that discrete functional habitat units (FHU) occur within river systems and that the spatial structure of FHU affects fish production. We present a method to delineate FHU using habitat maps, fish ecology, and spatial habitat characteristics. Utilizing a simulation model, we illustrate how modeling FHU structure of spawning and rearing habitat in a river system can improve our understanding of juvenile Atlantic salmon production dynamics. The FHU concept allows a flexible approach to more comprehensive analyses of the impacts of habitat alterations, seasonal habitat shifts, and spatial ecology of salmonids at various scales.

**Résumé** : Le saumon de l'Atlantique (*Salmo salar*) anadrome a un cycle vital complexe dans lequel l'espèce utilise des habitats qui s'inscrivent dans plusieurs échelles temporelles et spatiales. Bien que les halieutes aient étudié les divers éléments de l'habitat et les façons dont ils influent sur la croissance et la survie du saumon atlantique, ces études se concentrent typiquement sur les exigences du saumon en matière d'habitat durant un seul stade du cycle vital. Les progrès récents dans notre connaissance des populations de salmonidés dans les systèmes lotiques montrent que le fait d'ignorer le positionnement spatial des différents habitats et les capacités de dispersion des poissons d'un habitat à l'autre peut fausser les estimations de la qualité de l'habitat et de la production de saumon atlantique juvénile. À partir des concepts de juxtaposition et d'intercalation, nous formulons l'hypothèse que des unités fonctionnelles discrètes d'habitat sont présentes dans les systèmes fluviaux et que la structure spatiale de ces unités influe sur la production de poisson. Nous présentons une méthode permettant de délimiter les unités fonctionnelles d'habitat utilisant des cartes d'habitat, l'écologie du poisson et les caractéristiques spatiales des habitats. Au moyen d'un modèle de simulation, nous montrons comment la modélisation de la structure des unités fonctionnelles d'habitat des frayères et des alevinières dans un système fluvial peut accroître notre compréhension de la dynamique de la production des saumons atlantiques juvéniles. Le concept d'unités fonctionnelles d'habitat nous permet de réaliser avec souplesse des analyses plus détaillées des impacts des altérations des habitats, des changements saisonniers dans les habitats et de l'écologie spatiale des salmonidés à diverses échelles.

[Traduit par la Rédaction]

## Introduction

The conservation and restoration of Atlantic salmon (*Salmo salar*) populations in large river systems is an important task facing many fishery managers (Anonymous 1996). One crucial step towards achieving these goals is to optimize the numbers and quality of smolts produced by a

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spawning population in a river (Armstrong et al. 1998). To achieve optimal smolt production in streams, fishery managers may choose to manage their riverine habitat; this management may take the form of habitat protection, restoration, or enhancement. However, defining quantitative links between fish habitat and fish population dynamics has been difficult due to gaps in our understanding as to what constitutes habitat for a species and the appropriate scale at which habitat should be defined (Fausch and Young 1995; Grossman et al. 1995; Schlosser 1995; Hayes et al. 1996; Armstrong et al. 1998).

Anadromous Atlantic salmon exhibit a complex life history that requires the use of many different habitats that span many temporal and spatial scales. The environmental requirements of Atlantic salmon during their riverine life stages have been extensively studied and summarized (e.g., Bley 1987; Mills 1989; Shearer 1992; Gibson 1993; Gibson and Cutting 1993; Stanley and Trial 1995). Our review of

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this literature indicated that one aspect is clearly missing from the research on Atlantic salmon habitat use and preference — how the spatial relationships of different habitats for each life stage or season affects overall freshwater production of Atlantic salmon. We found that most of the salmonid literature focuses on specific habitat requirements for a particular life stage or season. There has been relatively little integration of this information across temporal and spatial scales as it relates to population dynamics. Recent studies in riverine systems indicate that habitat complementation (i.e., the spatial proximity of different nonsubstitutable resources) can be a critical factor determining the population size and persistence of fish populations (Scheimer et al. 1991; Dunning et al. 1992; Schlosser 1995). In addition, recent work on salmonid movements in streams has challenged the restricted movement paradigm that has driven analyses of salmonid habitat and population dynamics (Gowan et al. 1994). In combination, these two advances highlight the need to understand the role of the spatial arrangement of different habitat types necessary for fish production in streams. Our goal is to demonstrate that integrating recent advances in spatial habitat analysis with our improved understanding of salmonid movement in streams can facilitate selection of the appropriate scale for evaluating pre-smolt production of Atlantic salmon in streams and lead to better predictions of variability in that production.

## Natural units of scale: effects of habitat spacing and fish movement

To determine the appropriate scale at which to study a population segment, it is important to not only identify all of the habitat elements necessary to support every life history stage but also to examine how organisms move between these elements. In this century, wildlife ecology has intensively examined the importance of the spatial aspects of habitat. The work of Leopold (1933) introduced the concepts of habitat interspersion (degree of intermixing of discrete habitat types) and juxtaposition (relative location of discrete habitat types) to emphasize the importance of the spatial aspects of habitat. Over time, it has become a prevailing tenet of wildlife management that the overall suitability and productive capacity of habitat is determined by not only the quality and quantity of habitat for each life stage but also by the spatial relationship of these habitats (Thomas et al. 1979). Equally important is the realization that increased habitat heterogeneity favors edge species, while homogeneous habitat structure increases production of interior species (Thomas et al. 1979; Pearson et al. 1996). Wildlife management has not only embraced the importance of the spatial arrangement of habitat but has successfully used this information in routine management efforts to protect, restore, and enhance wildlife habitat and increase wildlife production (Thomas et al. 1979).

The importance of the spatial elements of habitat analyses were also identified early in fisheries ecology (Chapman 1966). However, the linkage between spatial analysis and fish population dynamics has recently gone through major theoretical advances (Fausch and Young 1995; Grossman et al. 1995; Schlosser 1995; Schlosser and Angermeier 1995). These studies advance the hypothesis that the spatial arrangements of habitat components is important in riverine systems and can give rise to markedly different fish population dynamics at a stream reach level and at larger mesohabitat scales (Grossman et al. 1995; Schlosser 1995). We believe that this hypothesis is well supported for salmonid populations. For example, higher salmonid growth rates occur in stream segments where adequate cover is in close proximity to an abundant food supply; conversely, production is lower in reaches where these two resources are widely separated (White 1991). These relationships likely exist at scales beyond the mesohabitat level because juvenile salmonids utilize different habitats at different life history stages and during different seasons (Symons and Heland 1978; Kennedy and Strange 1986; Cunjak 1988; Heggenes 1991; Heggenes and Borgstrom 1991; Kocik and Taylor 1995, 1996). While these shifts are well documented, population models that attempt to integrate spatial habitat differences are rare (cf. Fausch et al. 1988). A comprehensive model that does integrate these elements, SALMOD (Bartholow et al. 1993; Williamson et al. 1993), has not gained the widespread use of other habitat models such as the Instream Flow Incremental Methodology (Fausch et al. 1988).

The reasons for limited management-level utilization of spatial habitat analyses are elusive but seem related to the complexity of mapping entire river systems (Fausch et al. 1988) and a predominant notion that movement of stream fish was very limited (Gerking 1959; Bachman 1984). Recent technological advances in computer modeling and particularly Geographic Information Systems (GIS) technology are creating more accessible spatial databases and removing many of the analytical barriers that made comprehensive basinwide habitat assessment prohibitive (Isaak and Hubert 1997). More importantly, recent work on stream fish movement has challenged the restricted movement paradigm (RMP) that dominated stream ecology theory (Gowan et al. 1994; Schlosser 1995; Gowan and Fausch 1996). This rethinking of the movement of stream fishes suggests that it is important to get a better understanding of the scale of movement of fish at various life history stages and relate this to the habitat structure of a stream.

The consequences of the differing assumptions for fish mobility to the appropriate spatial scale become evident in a comparison of the RMP to the variable movement model (VMM) proposed by Gowan et al. (1994). Integrating these models suggests a gradient of dispersal patterns for salmonids. In all practical and theoretical examples, the location of redds serves as a geographic starting point for passive and active dispersal (Fig. 1). The RMP suggested that salmonids have relatively restricted movements from redds and isolation of family groups would be great (Fig. 1, Gerking 1959; Bachman 1984). Furthermore, the RMP classified moving fish as strays, transients, or nomads that were thought to contribute little to overall production (Gerking 1959; Chapman 1962; Jenkins 1969). For the RMP, the distribution of spawners would be a primary determinant of a river system's production potential within the habitat constraints of natural production units.

New research and re-analysis suggests that the RMP may not always apply and probably does not apply to large juvenile or adult salmonids (Gowan et al. 1994; Fausch and Young 1995). An extreme of the VMM is unlimited

**Fig. 1.** Three conceptual models of movement and dispersal of juvenile salmonids in streams and their consequences to spatial distribution and population dynamics. Within each panel the capital letter within an oval represents a redd and the lower case letters indicate dispersed juveniles. The left panel represents the RMP advanced by Gerking (1959). Two scenarios for the VMM of Gowan et al. (1994), constrained and unlimited movement are represented in the center and right panels, respectively.
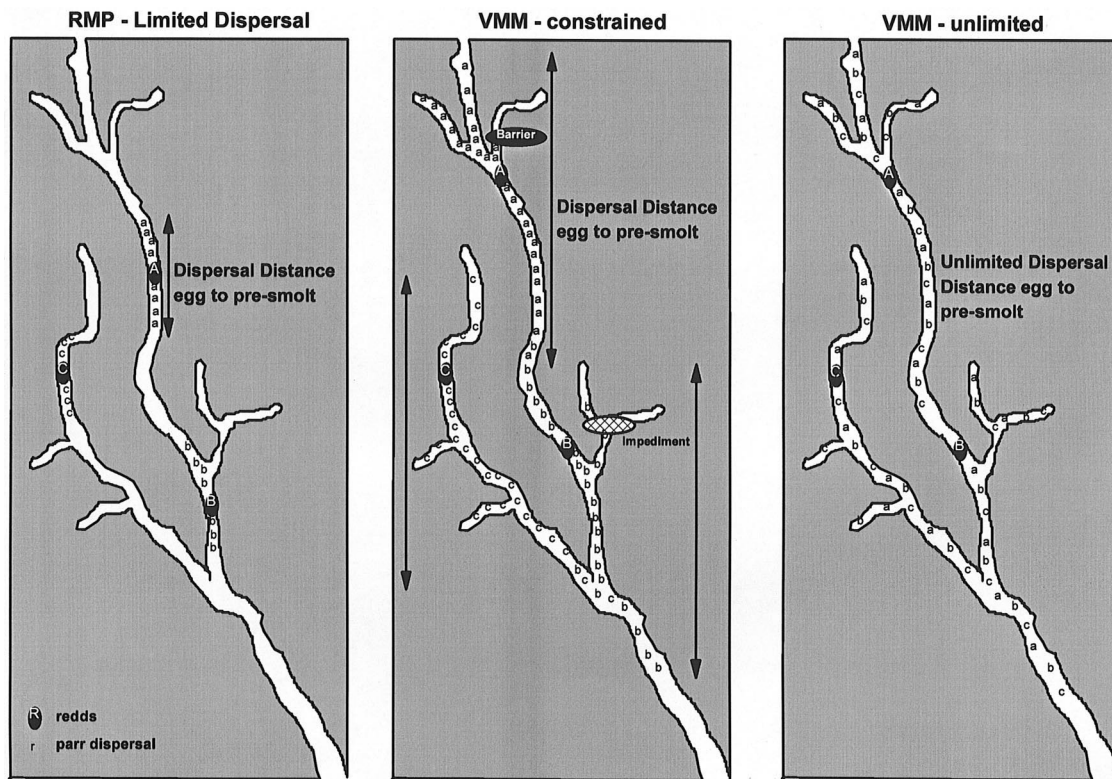


dispersal throughout a watershed (Fig. 1). Intermediate between the extremes of the RMP and unlimited model is a constrained VMM. In a constrained model, dispersal is limited by fish ecology and habitat characteristics. Typically for salmonids, the ability to move increases with size, resulting in a positive relationship between size/age and spatial scale (Gowan et al. 1994; Reeves et al. 1995). However, the ability to move may not be expressed to similar degrees under differential spatial distributions of habitat. In streams that have abundant and highly interspersed habitat for each life stage and season, movement is likely limited because fish do not need to move great distances to acquire requisite resources (Fausch and Young 1995; Schlosser 1995; Gowan and Fausch 1996; Behnke 1997). In streams where habitats are limited and (or) interspersion of necessary habitat types is low, movement is likely to be greater (Fausch and Young 1995; Schlosser 1995; Behnke 1997). Movement also has important genetic and behavioral elements in anadromous salmonids where a size threshold cues emigration from the river system. Another spatial element that influences movement is the location of habitat filters such as barriers or impediments that either totally limit or partially restrict movement. These filters could be natural (beaver dams, falls, stream order, longitudinal gradients, competing species, etc.) or anthropogenic (dams, diversions, changes in thermal regimes, dewatering, introduced species, etc.) and delineation of barriers could be abrupt (dam) or gradual (stream continuum). An additional point that determines the influence of each of these filters is that they may differen-

tially influence movement of juvenile and adult life stages. As a result, in the constrained VMM, the distribution of spawners and the associated movements of juveniles would be joint determinants of a river system's production potential within the habitat constraints of natural production units.

Through our synthesis of elements of spatial habitat structure and fish movement, we conclude that some variant of the constrained VMM is appropriate for most salmonid species, including Atlantic salmon at all life history stages. Furthermore, it seems that defining natural production units for life stages of interest would enhance our understanding of juvenile salmonid production because the structure and spatial distribution of these units would have important population dynamic ramifications. As fisheries scientists develop more sophisticated tools for habitat assessment and gain a better understanding of movement relative to habitat geography, delineating these units will become increasingly feasible. In the next section, we use Atlantic salmon as an example of how natural habitat units may be delineated to focus study on a spatial scale that is consistent with natural production units and may help better understand the interactions between population dynamics and habitat.

## Defining riverine production scale for Atlantic salmon parr

We hypothesize that basinwide estimates of salmonid abundance or assessment of habitat modifications on fish production could be improved by partitioning a river into

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natural production units that we call functional habitat units (FHU). FHU are natural partitions (strata) within river systems that contain the necessary habitat elements to support all life history stages through the life stage of interest. The boundaries of a FHU are defined by the spatial arrangement of discrete (spawning, fry, parr, seasonal, etc.) habitat elements, dispersal capabilities, and by filters (barriers or impediments) to dispersal. We view FHU for Atlantic salmon as a nested hierarchy of spatial scale that expands with progressive age/size from submetre (eggs) to global (adults). The FHU for parr production would likely be at a spatial scale between mesohabitat and subbasin for most systems (Williamson et al. 1993; Maxwell et al. 1995) and would contain all of the habitat elements necessary to support Atlantic salmon from the egg to pre-smolt stage. Another key element of the FHU is that the redd serves as the origin of a FHU and that the geographic placement of redds acts as a tether that constrains dispersal options. The goal of delineating these FHU (strata) is that similarities between production capacity, habitat elements, and spawning areas are maximized within FHU and differences are maximized between FHU.

To illustrate how interspersion, juxtaposition, and dispersal influence FHU structure and juvenile production, we present graphical models based on work with a GIS developed from habitat data for the Narraguagus River, Maine, U.S.A. (Beland et al. 1995; Kocik et al. unpublished data). In the Narraguagus River, much of the juvenile production habitat is not suitable for spawning as the substrate is either too large or embedded (Beland et al. 1982, 1995). Thus, spawning habitat is inclusive of rearing habitat but additional rearing habitat exists that cannot be used for spawning and is dependent solely upon parr dispersal. Upon examining habitat data for this river, we observed that the distribution of spawning and rearing habitat varies along the river's length. In the upstream section, spawning and rearing habitat are highly interspersed. In the downriver section, interspersion is lower and some of the rearing habitat is beyond the dispersal distances from larger spawning areas. To examine the role of dispersal upon FHU structure, we bounded Atlantic salmon movement from egg to pre-smolt using values from the literature (Heggenes and Borgstrom 1991; Beall et al. 1994). These studies suggest maximum Atlantic salmon dispersal of 0.4 km upstream and 1 km downstream with densities highest within 0.1 km upstream and 0.4 km downstream from the redd area, decreasing with distance from spawning areas. In addition, the presence of a lake in the middle of the river system forms a seasonal barrier to parr dispersal.

A visual model of FHU delineation can be illustrated by examining a simple stream reach (Fig. 2). In this example, two areas with the same ratio of spawner to juvenile habitat (1:6) and total juvenile habitat (5000 m$^2$) likely have very different juvenile recruitment dynamics. In the first example, interspersion and juxtaposition are favorable with two spawning areas separated by 1.5 km (Fig. 2A). In this example, a total of 1440 m$^2$ of river habitat would not be subject to parr dispersal given full utilization of spawning habitat and maximum dispersal distances. This illustrates a natural delineation between upstream and downstream production areas with no overlap in juvenile production. Hence, there

are two FHU with juvenile production areas of 1800 m$^2$ each for a total of 3600 m$^2$ of utilized habitat.

With a lower interspersion of the two habitat types, all the spawning habitat is restricted to the upper river (Fig. 2B). In this scenario, only 2200 m$^2$ of the stream would be utilized by spawners in a single FHU. Over 55% of available juvenile production habitat is beyond the documented dispersal maximum. This example illustrates the importance of interspersion of two habitat types and the consequences of juxtaposition. Most habitat models would treat the habitat quality of these two stream sections as equivalent, but including spatial interactions makes it apparent that the stream reach with favorable spatial attributes has the potential to produce 1.6 times the juveniles as the other reach.

To bring these analytical techniques to a watershed level, it is necessary to use GIS to allow more accurate measurements and accounting of river sinuosity. However, the delineation of these units is conducted in the same manner presented above using the spatial arrangement of spawning and juvenile habitat and the assumed dispersal limits. Once GIS data are developed, they can be presented by graphing the parr dispersal area, scaled to spawning area, along the longitudinal gradient of the river (Fig. 3). Such a graph illustrates the interaction of interspersion, juxtaposition, and dispersal capabilities in bounding juvenile production zones (Fig. 3). This graph not only shows the distinctness of the zones but also the magnitude of spawning area that supports production in each one. For example, zone A is 1.5 km long (from river km 6.7 to river km 8.2) and is 9 m longer than zone B but the spawning area contained in zone B (144 metric units) is 2 times greater than that of zone A (72 metric units). This is apparent in the larger area under the curve. In this example, we identified 10 distinct production zones. To simplify simulations for illustrative purposes in the spatial model below, we combined these zones into downstream (zones A–F) and upstream (zones G–J) FHU of the mainstem river.

## A spatial model for FHU

To explore the impact of differing FHU structure on pre-smolt production within a river, we constructed a simple, four-step simulation model (Fig. 4) using a Microsoft Excel workbook format utilizing risk analysis software (@Risk; Palisade 1996). This simulation approach allowed sampling of model parameters from normal or uniform distributions using Latin Hypercube sampling and variable recalculation using Monte Carlo sampling (Palisade 1996). The model is purposefully uncomplicated in order to limit the assumptions needed and focus on the impact of assumptions regarding the spatial arrangement of habitat and spawners.

To start the model, we use the number of female spawners observed in the Narraguagus River system in the autumn of 1996 as the initial condition for generation 0 (K.F. Beland, Maine Atlantic Salmon Authority, Bangor, ME, U.S.A., personal communication). Step 1 of the model determines potential egg deposition by multiplying the number of females by a fecundity variable selected from a normal distribution of the effective fecundity (mean 7560 and SE 1000) for Narraguagus River Atlantic salmon (Baum and Meister 1971).

**Fig. 2.** A graphical representation of the effects of the interspersion and juxtaposition of spawning and nursery habitats upon juvenile production potential in two hypothetical stream reaches with 5000 m$^2$ of parr habitat and 800 m$^2$ of spawning habitat. In Reach A, spawning habitat is in two separate regions and dispersal results in two FHU with a net production area of 3600 m$^2$. In reach B, all spawning habitat is in one reach and dispersal ranges result in single FHU with a net production area of only 2200 m$^2$.
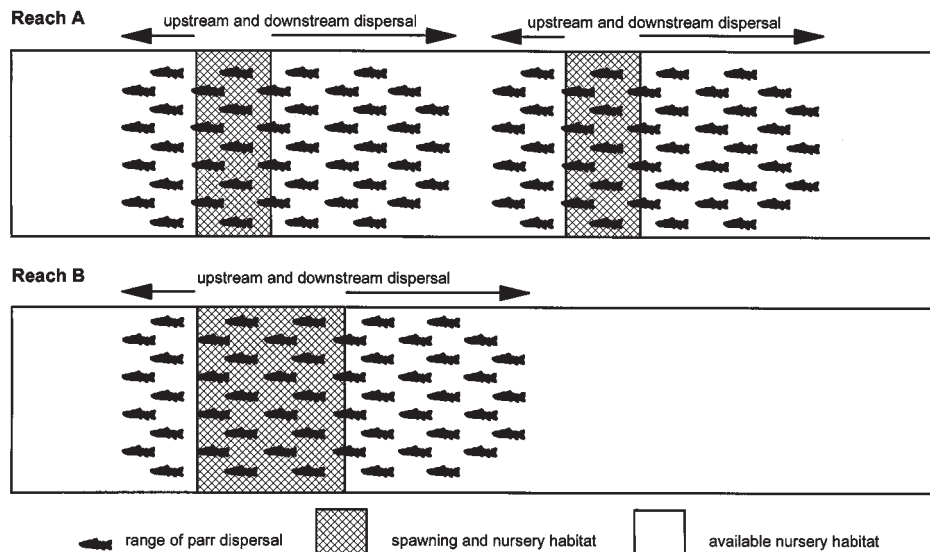


We calculate parr production from potential egg deposition using a modified version of a linear regression model for a neighboring river (Beland 1996). Because of recent low escapement levels in Maine, no data are available to describe the asymptote of this relationship. To compensate, we capped parr production at 7 parr per metric unit, a level chosen based on maximum densities observed in discrete reaches of Maine salmon rivers since 1950 (K.F. Beland, Maine Atlantic Salmon Authority, Bangor, ME, U.S.A., personal communication). Thus, the resulting algorithm at step 2 becomes a linear regression model with associated standard error (parr = 0.0213 eggs + 1605.04, ±2492 SE) that is truncated by a lower bound of 0 and an upper bound that is determined by the amount of available habitat (Fig. 4). This approach follows the recommendation that a recruitment relationship is a proxy for total habitat quality (Hayes et al. 1996).

At step 3, we calculate the number of outmigrating smolts by multiplying parr production by an overwinter survival estimate selected from a uniform distribution (25 to 60%) based on other studies in New England (Orciari et al. 1994; Whalen et al. 1996). At step 4, we calculate total adult returns by multiplying total smolt production by a marine survival variable selected from a uniform distribution (0.75% to 5%) based on the range of values in the literature and recent simulation studies on the Narraguagus River (Bley and Moring 1988; Anonymous 1996; Friedland 1998). The final output for the initial generation becomes the input for the next generation and continued for 50 successive generations. Additional assumptions of this model are a 1:1 sex ratio and no cross-over of age classes (smolt at age-2 and return as 2 sea-winter adults). We chose this approach because deviations from this life history pattern are minimal and tests with more complicated overlapping age-classes yielded similar results.
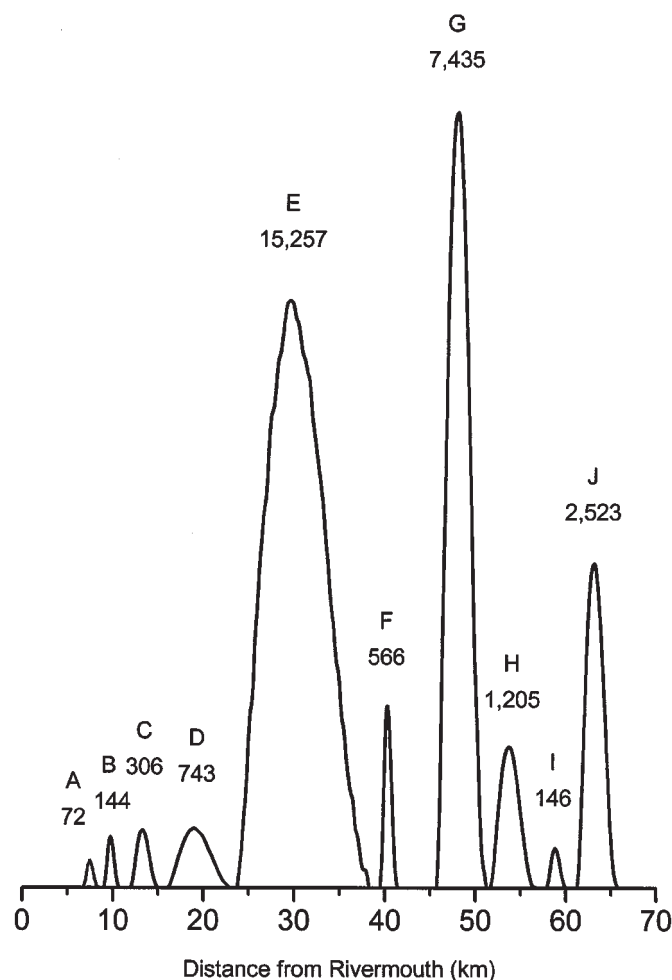
Each iteration of the simulation was run until the population was extirpated or reached 50 generations. Three sum-

mary variables provide useful indices of the results: extirpation probability, average parr production, and generations to recover. The extirpation probability is the likelihood that the population will fall below two spawners within 50 generations. When the population survived, a useful index value was the average parr production over 50 generations. This value represents the juvenile production capacity and is presented with its standard deviation and coefficient of variation. Our final index value was generations to recover; this value was the number of generations for parr production to reach the mean parr production level for that iteration. All simulations were run until these three output variables converged at variance levels of less than the 1.5% level; for most simulations this was between 1800 and 2000 iterations.

To explore the impact of ignoring the importance of habitat interspersion and juxtaposition in delineating FHU, we ran a baseline simulation that treated the Narraguagus River as a single FHU (Fig. 4) comprised of 6017 metric units (1 metric unit = 100 m$^2$) of parr habitat. This baseline simulation for the Narraguagus River parr habitat yielded an extirpation probability of 17.8% and production averaged 15 552 (±4 456) Atlantic salmon parr (Table 1). Because our study river exhibits few filters to adult dispersal but contains spatial filters to juvenile dispersal, we felt it was important to examine a scenario of unlimited adult access with habitat constrained juvenile dispersal. As such, we partitioned the 6017 metric units of parr habitat into three distinct FHU based on previous habitat research in the Narraguagus River (Beland et al. 1995; Fig. 5; Table 1). The majority of juvenile production habitat is located in the mainstem with 3544 metric units in the lower mainstem FHU and 1989 metric units in the upper mainstem FHU. The west branch FHU constitutes 484 metric units, or 8%, of the basinwide total.

Because no definitive model for within-river dispersal of spawners is available, we explored the implications of four spawner distribution scenarios (homing, preference, propor-

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**Fig. 3.** A generalized graphical representation of juvenile distribution zones and associated spawning areas in Narraguagus River mainstem reaches based on original data from Beland et al. (1995). The X-axis represents the distance upstream from the head of tide; the distance along this axis for each zone represents the upstream and downstream dispersal of juveniles from connected spawning and rearing areas. The area under each hyperbola is proportional to the total spawning area in that production zone and is listed above each curve in metric units (1 unit = 100 m$^2$).



observed in the Narraguagus River system in the autumn of 1996 (K.F. Beland, Maine Atlantic Salmon Authority, Bangor, ME, U.S.A., personal communication).

Results from this group of simulations indicate that artificially grouping FHU, as in the baseline scenario, would potentially overestimate extirpation probability and generations-to-recover while underestimating long-term parr production capabilities (Table 1). Different scenarios of the spatial distribution of adults highlights the potential effects of varying these assumptions (Table 1). The magnitude of these assumptions is compelling as it suggests a 48% increase in juvenile production potential and near 60-fold difference in extirpation probabilities between the baseline and proportional models. Differences between the intermediate models are also substantial. The results of these simulations suggest that understanding FHU structure and the factors that regulate site-selection by spawners will allow for significant increases in the precision of production estimates and population dynamics analyses.

## Discussion

As theory regarding the mobility of juvenile salmonids in streams has evolved (Gowan et al. 1994; Gowan and Fausch 1996), the importance of determining the appropriate scale for assessing parr production and population dynamics emerges as critical for accurate determination of basin-scale production dynamics. Our simulations of Atlantic salmon parr production in the Narraguagus River show that segmentation of a basin into distinct FHU, relevant to the juvenile stage, lends stability to population structure within a riverine stock and leads to less variation in estimates of total parr production in the basin. We believe that this is particularly true of anadromous salmonids because adults can pass habitat filters that juveniles may not be able to pass physically or behaviorally, thus bounding FHU for juvenile production. These conclusions are analogous to those for metapopulations that examine the demographic stability between populations or stocks (e.g., Schlosser 1995; Schlosser and Angermeier 1995). However, the stability that is exhibited by increased FHU complexity is driven by habitat-based spatial segregation within a stock across a spatially complex habitat. The two key assumptions of this stratification are that isolated segments of juvenile rearing habitat exist and that biotic potential (eggs) is determined by spawning site selection that is more complex than simple homing.

Some fragmentation or isolation of distinct habitat areas for juvenile production is likely common in most watersheds large enough to sustain a stock in relative isolation leading to multiple FHU within a river system. While at the extreme the genetic isolation of these units would establish stocks, restricted juvenile dispersal within a stock at the FHU level would provide buffers to environmental extremes at the basinwide level. The reasons for increased stability and production potential are two-fold. First, even at low spawner densities, if all fish spawned in one area, density-dependent factors would lead to decreased production as compared to a population with dispersed spawners. Second, the filters and other parameters that delineate FHU structure often result in units that react differently to extreme environmental conditions. For example, an upstream FHU may be more suitable

tional, and semi-random). The homing scenario assumed that the number of females returning to each FHU varied based on previous parr production in each FHU. The preference scenario assumed that spawners have a general preference for individual FHU based on distance from the ocean and FHU spawner density. We simulated this scenario using a three-tiered function with a density dependent sequential preference for the lower mainstem, upper mainstem, and west branch FHU. The proportional scenario allocated females using constant proportions based on total spawning habitat in each reach. The semi-random scenario allocated spawners first based on a 0–8% probability of spawning in the west branch FHU and then by a 0 to 92–100% probability of spawning in the lower mainstem or upper mainstem FHU. For initial model inputs we used the actual geographic distribution of female spawners, represented by redd counts

**Table 1.** Index values of simulation models of Atlantic salmon populations for extirpation probability, generations to recover, average parr production (years 1–50) with its associated standard deviation and coefficient of variation (C.V.).

| Model name | Extirpation probability (%) | Generations to recover | Parr production | Standard deviation | C.V. (%) |
|---|---|---|---|---|---|
| Single FHU – baseline | 17.8 | 18.7 | 15 552 | 4456 | 28.65 |
| 3 FHU – homing | 7.4 | 14.8 | 18 570 | 4649 | 25.04 |
| 3 FHU – semi-random | 2.6 | 15.2 | 18 827 | 2285 | 12.14 |
| 3 FHU – preference | 1.4 | 15.4 | 20 363 | 2343 | 11.51 |
| 3 FHU – proportional | 0.3 | 7.8 | 23 096 | 2096 | 9.08 |

**Fig. 4.** Flow chart and schematic of a basic simulation model of juvenile Atlantic salmon production on a watershed scale. The model is initiated with the number of female spawners present in year 0. Resultant output from one generation of the model are the starting values for the next generation.
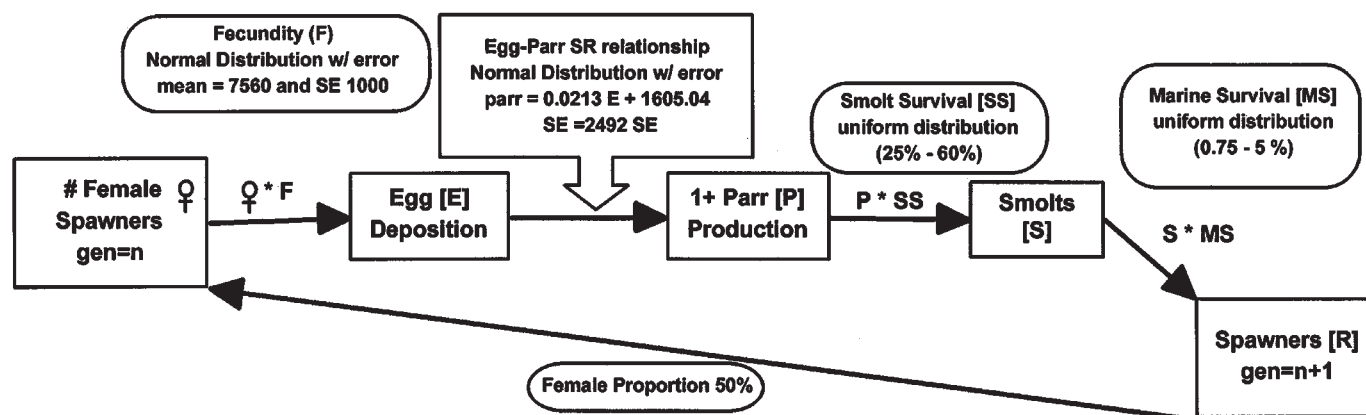


**Fig. 5.** Flow chart of a simulation model of juvenile Atlantic salmon production with variable spawner dispersal between three distinct FHU of juvenile production within a watershed.
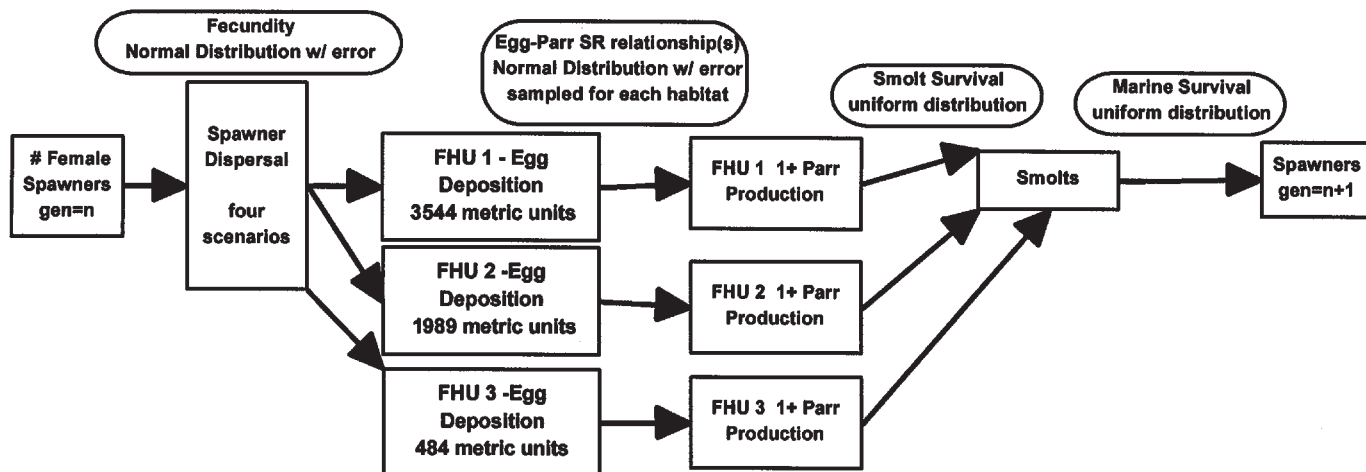


during a warm wet summer while a downstream FHU is more suitable during a dry cool summer. As such, these habitat units would respond differently to different environmental conditions. These differential responses act to dampen the overall effects of environmental extremes within a basin. Our simulation results underscore these points, suggesting that, for Atlantic salmon, the presence of multiple FHU within a river basin is beneficial to persistence at low population levels and leads to increased juvenile production. As a result, a more complex FHU structure would serve to make a population more productive and stable over time. However, excessive fragmentation is also of concern since the amount of critical habitat can become too isolated from other habitats to maintain adequate linkage (spawner dispersal) between the habitat units.

In the Narraguagus River example, FHU delineations are primarily a consequence of natural geological structure. In other systems, these delineations may be driven primarily by anthropogenic effects — the presence of impoundments, alteration of channel structure, instream flow issues, etc. A

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frequent conclusion of studies of the spatial elements of fish habitat is that habitat fragmentation is a major problem (Schlosser 1991; Lohr and Fausch 1997; Schlosser and Angermeier 1995). Loss of connectivity and complete isolation of stream reaches are obvious and chronic detriments to the natural structure of stream fish communities. Using the FHU approach, the challenge to fishery managers in perturbed systems would be to determine the extent to which anthropogenic factors have either fragmented the habitat (separated FHU that were previously contiguous) or simplified habitat (decreased FHU number and inter-FHU differences) from baseline conditions. Clearly, as the quality of the habitat degrades in even one FHU, total juvenile production in the river decreases. This is an important consideration because decreased production could be the result of reduced habitat quality in only part of a watershed (i.e., only in one FHU). If habitat is degraded in a preferred spawning reach, these changes will be further accentuated. As such, using a FHU approach could identify a geographic area of greatest production significance, focusing habitat rehabilitation efforts or protection efforts where they are needed the most.

Our simulations also suggest that changes in overall smolt production are caused not only by changes in FHU complexity within the basin but also by changes in spawner distribution patterns between the FHU. The optimal theoretical model of distribution appears to be a proportional model since the extinction probability and generations to recover are lowest and long-term parr production are the highest with low variation. However, this model may be difficult to defend biologically as it requires a population of spawners to distribute itself optimally in relation to available habitat within the basin (Bartholow et al. 1993; Williamson et al. 1993). Thus, a combination of the preference and semi-random models may best explain the distribution of redds among FHU. We believe that there is strong evidence that spawning site choice by salmonid populations within rivers is influenced by discharge, temperature, and spawner density, as well as natal stream reach (Kocik and Taylor 1987). Given this hypothesis, if spawner distributions between FHU (defined at the juvenile scale) can be quantified and related to demographic, behavioral, or environmental factors, the variance of stock-recruitment relationships may be decreased and a better understanding of basinwide dynamics will occur. In addition, this has important management ramifications for establishing target spawning requirements that frequently disregard spatial distribution (O'Connell and Dempson 1995). For example, spawning targets for Atlantic salmon are often based on desired egg deposition rates and the fecundity of females. If spawner levels in excess of this threshold are needed to distribute spawners throughout all reaches of the watershed, the target levels may be insufficient.

Through our synthesis of recent developments in spatial analysis of fish habitat, salmonid ecology, and salmonid movement in streams, we conclude that Atlantic salmon populations likely function in a manner that supports the hypothesis that the spatial arrangements of habitat components can give rise to markedly different population dynamics at various spatial scales (Grossman et al. 1995; Schlosser 1995). An interesting component of this hypothesis is that it highlights the need to integrate physical habitat data with traditional population dynamics (mortality, fecundity, immigration, and emigration). Additionally, a spatial approach should become a mechanism to broaden habitat models and move away from the general assumption that fish populations are solely limited by physical habitat to a more holistic approach that integrates biotic factors such as competition, predation, and fisheries (Fausch et al. 1988; Hayes et al. 1996).

We believe that the FHU approach provides a framework that uses the spatial distributions of habitat in concert with data on stage-specific habitat utilization, dispersal, and habitat filters to define natural units at various scales. The advent of more precise and user-friendly methods for measuring, interpreting, and modeling habitat (i.e., global positioning systems and GIS; Isaak and Hubert 1997) provide new opportunities for analysis at various spatial scales. These new methods will enable researchers to quantitatively examine differences in salmonid production to assess the impact of interspersion and juxtaposition of discrete habitat units within and between FHU. While the case-study explored in this manuscript highlighted primarily the abiotic elements of habitat, FHU structure should also be defined by the occurrence of biotic factors that would restrict fish distribution ranging from diseases to competing fish species to avian or mammalian predators. The baseline habitat, movement, and ecological data needed to delineate FHU is substantial, but when these data are available, determining appropriate scale for a life stage will improve resolution of analyses of population dynamics, habitat management, and other evaluations that assume a closed population or population segment.

## References

Anonymous. 1996. Report of the Working Group on North Atlantic Salmon. Copenhagen, 10–19 April 1999. ICES, Doc. C.M. 1996/Assess: 11.

Armstrong, J.D., Grant, J.W.A., Forsgren, H.L., Fausch, K.D., DeGraaf, R.M., Fleming, I.A., Prowse, T.D., and Schlosser, I.J. 1998. The application of science to the management of Atlantic salmon (*Salmo salar*): integration across scales. Can. J. Fish. Aquat. Sci. **55**(Suppl. 1): 303–311.

Bachman, R.A. 1984. Foraging behavior of free-ranging wild and hatchery brown trout in a stream. Trans. Am. Fish. Soc. **113**: 1–32.

Bartholow, J.M., Laake, J.L, Stalnaker, C.B., and Williamson, S.C. 1993. A salmonid population model with emphasis on habitat limitations. Rivers, **4**: 265–279.

Baum, E.T., and Meister, A.L. 1971. Fecundity of Atlantic salmon (*Salmo salar*) from two Maine rivers. J. Fish. Res. Board Can. **28**: 764–767.

Beall, E., Dumas, J., Claireaux, D., Barrière, L., and Marty, C. 1994. Dispersal patterns and survival of Atlantic salmon (*Salmo salar* L.) juveniles in a nursery stream. ICES J. Mar. Sci. **51**: 1–9.

Behnke, R.J. 1997. About Trout. Trout. Autumn: 37–39.

Beland, K.F., Jordan, R.M., and Meister, A.L. 1982. Water depth and velocity preferences of spawning Atlantic salmon in Maine rivers. N. Am. J. Fish. Manage. **2**: 11–13.

Beland, K.F. 1996. The relationship between redd counts and Atlantic salmon (*Salmo salar*) parr populations in the Dennys River, Maine. Can. J. Fish. Aquat. Sci. **53**: 513–519, Erratum **53**: 2394.

Beland, K.F., Dubé, N.R., Evers, M., Spencer, R.C., Thomas, S., Vander Haegen, G., and Baum, E.T. 1995. Atlantic salmon research addressing issues of concern to the National Marine Fisheries Service and Atlantic Sea Run Salmon Commission. Final Project Report NA29FL0131-01. Bangor, Me. 133 p.

Bley, P.W. 1987. Age, growth, and mortality of juvenile Atlantic salmon in streams: a review. U.S. Fish Wildl. Ser., Biol. Rep. 87(4). 25 p.

Bley, P.W., and J.R. Moring. 1988. Freshwater and ocean survival of Atlantic salmon and steelhead. U.S. Fish Wildl. Ser., Biol. Rep. 88(9): 21 p.

Chapman, D.W. 1962. Aggressive behavior in juvenile coho salmon as a cause of emigration. J. Fish. Res. Board Can. **19:** 1047–1080.

Chapman D.W. 1966. Food and space as regulators of salmonid populations in streams. Am. Nat. **100**: 345–57.

Cunjak, R.A. 1988. Behaviour and microhabitat of young Atlantic salmon (*Salmo salar*) during winter. Can. J. Fish. Aquat. Sci. **45**: 2156–2160.

Dunning, J.B., Danielson, J.B., and Pulliam, H.R. 1992. Ecological processes that affect populations in complex landscapes. Oikos, **65**: 169–175.

Fausch, K.D., and Young, M.K. 1995. Evolutionary significant units and movement of resident stream fishes: a cautionary tale. *In* Evolution and the aquatic ecosystem: defining unique units in population conservation. *Edited by* J. Nielsen. Am. Fish. Soc. Symp. **17**: 360–370.

Fausch, K.D., Hawkes, C.L., and Parsons, M.G. 1988. Models that predict standing crop of stream fish from habitat variables: 1950–85. U.S.D.A. For. Serv. Pac. N.W. Res. Stn. Gen. Tech. Rep. PNW-GTR-213. 52 p.

Friedland, K.D. 1998. Ocean climate influences on critical Atlantic salmon (*Salmo salar*) life history events. Can. J. Fish. Aquat. Sci. **55**(Suppl. 1): 119–130.

Gerking, S.D. 1959. The restricted movement of fish populations. Biol. Rev. **34**: 221–242.

Gibson, R.J. 1993. The Atlantic salmon in fresh water: spawning, rearing and production. Rev. Fish Biol. Fish. **3**: 39–73.

Gibson, R.J., and Cutting, R.E. (*Editors*). 1993. Production of juvenile Atlantic salmon, *Salmo salar,* in natural waters. Can. Spec. Publ. Fish. Aquat. Sci. 118.

Gowan, C., and Fausch, K.D. 1996. Mobile brook trout in two high-elevation Colorado streams: re-evaluating the concept of restricted movement. Can. J. Fish. Aquat. Sci. **53**: 1370–1381.

Gowan, C., Young, M.K., Fausch, K.D., and Riley, S.C. 1994. Restricted movement in resident stream salmonids: a paradigm lost? Can. J. Fish. Aquat. Sci. **51**: 2626–2637.

Grossman, G.D., Hill, J., and Petty, J.T. 1995. Observations on habitat structure, population regulation, and habitat use with respect to evolutionary significant units: a landscape perspective for lotic systems. *In* Evolution and the aquatic ecosystem: defining unique units in population conservation. *Edited by* J. Nielsen. Am. Fish. Soc. Symp. **17**: 381–391.

Hayes, D.B., Ferreri, C.P., and Taylor, W.W. 1996. Linking fish habitat to their population dynamics. Can. J. Fish. Aquat. Sci. **53**(Suppl 1): 383–390.

Heggenes, J. 1991. Comparisons of habitat availability and habitat use by an allopatric cohort of juvenile Atlantic salmon *Salmo salar* under conditions of low competition in a Norwegian stream. Holarct. Ecol. **14**: 51–62.

Heggenes, J., and Borgstrom, R. 1991. Effect of habitat types on survival, spatial distribution and production of an allopatric cohort of Atlantic salmon, *Salmo salar* L., under conditions of low competition. J. Fish Biol. **38**: 267–280.

Isaak, D.J., and Hubert, W.A. 1997. Integrating new technologies into fisheries science: the application of Geographic Information Systems. Fisheries, **22**: 6–10.

Jenkins, T.M. 1969. Social structure, position choice and microdistribution of two trout species (*Salmo trutta* and *Salmo gairdneri*) resident in mountain streams. Anim. Behav. Monogr. **2**: 56–123.

Kennedy, G.J.A., and Strange, C.D. 1986. The effects of intra and inter-specific competition on the distribution of stocked juvenile Atlantic salmon, *Salmo salar* L., in relation to depth and gradient in an upland trout *Salmo trutta* L. stream. J. Fish Biol. **29**: 199–214.

Kocik, J.F., and Taylor, W.W. 1987. The effect of fall and winter instream flow on year-class strength in Pacific salmon evolutionarily adapted to early fry outmigration: A Great Lakes perspective. Common strategies of anadromous and catadromous fishes. Am. Fish. Soc. Symp. **1**: 430–440.

Kocik, J.F., and Taylor, W.W. 1995. Effect of juvenile steelhead (*Oncorhynchus mykiss*) on age-0 and age-1 brown trout (*Salmo trutta*) survival and growth in a sympatric nursery stream. Can. J. Fish. Aquat. Sci. **52**: 105–114.

Kocik, J.F., and Taylor, W.W. 1996. Effect of juvenile steelhead on juvenile brown trout habitat use in a low-gradient Great Lakes tributary. Trans. Am. Fish. Soc. **125**: 244–252.

Leopold, A. 1933. Game Management. The University of Wisconsin Press. Madison, Wisc.

Lohr, S.C., and Fausch, K.D. 1997. Multiscale analysis of natural variability in stream fish assemblages of a western Great Plains watershed. Copeia, **1997**(4): 706–724.

Maxwell, J.R., Edwards, C.E., Jensen, M.E., Paustian, S.J., Parrott, H., and Hill, D.M. 1995. A hierarchical framework of aquatic ecology units in North America (Neararctic Zone). U.S.D.A. For. Serv. N. Central For. Exp. Stn. Gen. Tech. Rep. NC-176. 72 p.

Mills, D. 1989. Ecology and management of Atlantic salmon. Chapman and Hull, London and New York.

O'Connell, M.F., and Dempson, J.B. 1995. Target spawning requirements for Atlantic salmon, *Salmo salar* L., in Newfoundland rivers. Fish. Manage. Ecol. **2**: 161–170.

Orciari, R.D., Leonard, G.H., Mysling, D.J., and Schluntz, E.C. 1994. Survival, growth, and smolt production of Atlantic salmon stocked as fry in a southern New England stream. N. Am. J. Fish. Manage. **14**: 588–606.

Palisade Corporation. 1996. Guide to using @risk risk analysis and simulation add-in for Microsoft Excel or Lotus 1-2-3. New Field, New York. 296 p.

Pearson, S.M., Turner, M.G., Gardner, R.H., and O'Neill, R.V. 1996. An organism-based perspective of habitat fragmentation. *In* Biodiversity in managed landscapes: theory and practice. *Edited by* R.C. Szaro and D.W. Johnston. Oxford University Press, New York. pp. 77–95.

Reeves, G.H., Benda, L.E., Burnett, K.M., Bisson, P.A., and Sedell, J.R. 1995. A disturbance-based ecosystem approach to

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maintaining and restoring freshwater habitats of evolutionary significant units of anadromous salmonids in the Pacific northwest. *In* Evolution and the aquatic ecosystem: defining unique units in population conservation. *Edited by* J. Nielsen. Am. Fish. Soc. Symp. **17**: 334–349.

Scheimer, F., Spindler, T., Wintersberger, H., Schneider, A., and Chovanec, A. 1991. Fish fry associations: important indicators for the ecological status of large rivers. Verh. Int. Ver. Limnol. **24**: 2497–2500.

Schlosser, I.J. 1991. Stream fish ecology: a landscape perspective. BioScience, **41**: 704–712.

Schlosser, I.J. 1995. Critical landscape attributes that influence fish population dynamics in headwater streams. Hydrobiologia, **303**: 71–81.

Schlosser, I.J., and Angermeier, P.L. 1995. Spatial variation in demographic processes of lotic fishes: conceptual models, empirical evidence, and implications for conservation. *In* Evolution and the aquatic ecosystem: defining unique units in population conservation. *Edited by* J. Nielsen. Am. Fish. Soc. Symp. **17**: 392–401

Shearer, W.M. 1992. The Atlantic salmon. University Press, Cambridge. 244 p.

Stanley, J.G., and Trial, J.G. 1995. Habitat suitability index models: nonmigratory freshwater life stages of Atlantic salmon. U.S. DOI, Biol. Sci. Rep. 3.

Symons, P.E.K., and Heland, M. 1978. Stream habitats and behavioral interactions of underyearling and yearling Atlantic salmon (*Salmo salar*). J. Fish. Res. Board Can. **35**: 175–183.

Thomas, J.W., Black, H., Scherzinger, R.J., and Petersen, R.J. 1979. Deer and elk. *In* Wildlife habitats in managed forests, the Blue Mountains of Oregon and Washington. *Edited by* J.W. Thomas. U.S.D.A. Forest Service Agriculture Handbook 553. pp. 104–127.

Whalen, K.G., Parrish, D.L., and Mather, M.E. 1996. Factors influencing overwinter mortality and downstream migration of Atlantic salmon in Vermont tributaries of the Connecticut River. Final Report. National Marine Fisheries Service Anadromous Fish Conservation Act NA46FA0126, Amherst, Mass. 49 p.

White, R.J. 1991. Resisted lateral scour in streams — its special importance to salmonid habitat and management. *In* Fisheries Bioengineering Symposium. *Edited by* R.J. White and J. Colt. AFS Spec. Symp. 10. pp. 200–203.

Williamson, S.C., Bartholow, J.M., and Stalnaker, C.B. 1993. Conceptual model for quantifying pre-smolt production from flow-dependant physical habitat and water temperature. Reg. Rivers: Res. Manage. **8**: 15–28.