

# Multi-scale determinants of secondary production in Atlantic salmon (*Salmo salar*) streams

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**Abstract:** Understanding variation in the freshwater production of Atlantic salmon across its range is a critical aspect of the species' conservation, restoration, and management. We focus on how environmental factors operate at four hierarchical scales (region, watershed, reach, local habitat) to influence the production and survivorship of juvenile salmon and the production of their invertebrate food base. Using published, quantitative information about invertebrate production in small, cold streams characteristic of Atlantic salmon nursery streams, we estimate expected maximum salmon production will be ca. 9 (range 6–22) g wet mass · m<sup>-2</sup> · year<sup>-1</sup>, which compares favorably with reported literature values of <1 to 17 g · m<sup>-2</sup>. We highlight some empirically based, shortcut approaches to estimating invertebrate production that may be particularly useful for evaluating salmonid production across a range of scales. We also consider how availability of invertebrate prey may influence salmon production. As a synthesis, we integrate existing information into a multi-scale framework by making qualitative predictions (hypotheses) about expected patterns of invertebrate and salmon production at different habitat scales. We then develop quantitative, heuristic scenarios that predict (hypothesize) how salmon and invertebrate production will change in response to selected physicochemical and non-trophic habitat limitations operating at the watershed (geology, land use) and reach (channel form, canopy) scales. Predicted values, which fall within the range of observed values for Atlantic salmon streams, demonstrate that a multi-scale habitat perspective can provide important insights into local to regional variation in the production of Atlantic salmon across its range and thus contribute to Atlantic salmon conservation, restoration, and management.

**Résumé :** Il est primordial de comprendre la variation dans la production dulcicole du saumon atlantique dans son aire de répartition pour assurer la conservation, le rétablissement et la gestion de cette espèce. Nous mettons l'accent sur la manière dont les facteurs environnementaux agissent à quatre échelles hiérarchiques (région, bassin, tronçon de cours d'eau et habitat) pour influencer la production et la survie des saumons juvéniles, de même que sur la production des invertébrés dont ils se nourrissent. À l'aide de données quantitatives publiées sur la production d'invertébrés dans les petits cours d'eau froids qui constituent typiquement les alevinières du saumon atlantique, nous estimons la production de saumon maximale attendue à environ 9 (fourchette de 6 à 22) g de poids frais par m<sup>2</sup> et par année, ce qui se compare favorablement aux valeurs signalées dans la documentation scientifique (<1–17 g · m<sup>-2</sup>). Nous présentons des méthodes empiriques abrégées d'estimation de la production d'invertébrés qui peuvent être particulièrement utiles pour évaluer la production de salmonidés à diverses échelles. Nous examinons aussi comment la disponibilité des invertébrés proies peut influencer sur la production de saumons. À titre de synthèse, nous constituons avec les données existantes un cadre multi-échelles en faisant des prévisions qualitatives (hypothèses) concernant les profils attendus de production d'invertébrés et de saumons à différentes échelles d'habitat. Nous établissons par la suite des scénarios heuristiques quantitatifs qui prévoient (de manière hypothétique) comment la production d'invertébrés et de saumons changera en fonction de facteurs physicochimiques et non trophiques limitants liés à l'habitat et agissant aux échelles des bassins (géologie, utilisation des terres) et des tronçons de cours d'eau (forme du chenal, couvert végétal). Les valeurs prévues, qui tombent dans la fourchette des valeurs observées pour les cours d'eau à saumon atlantique, montrent qu'une approche prenant en compte l'habitat à diverses échelles peut fournir des perspectives intéressantes sur la variation aux échelles locale à régionale de la production du saumon atlantique dans l'ensemble de son aire de répartition, et ainsi contribuer à la conservation, au rétablissement et à la gestion de l'espèce.

[Traduit par la Rédaction]

## Introduction

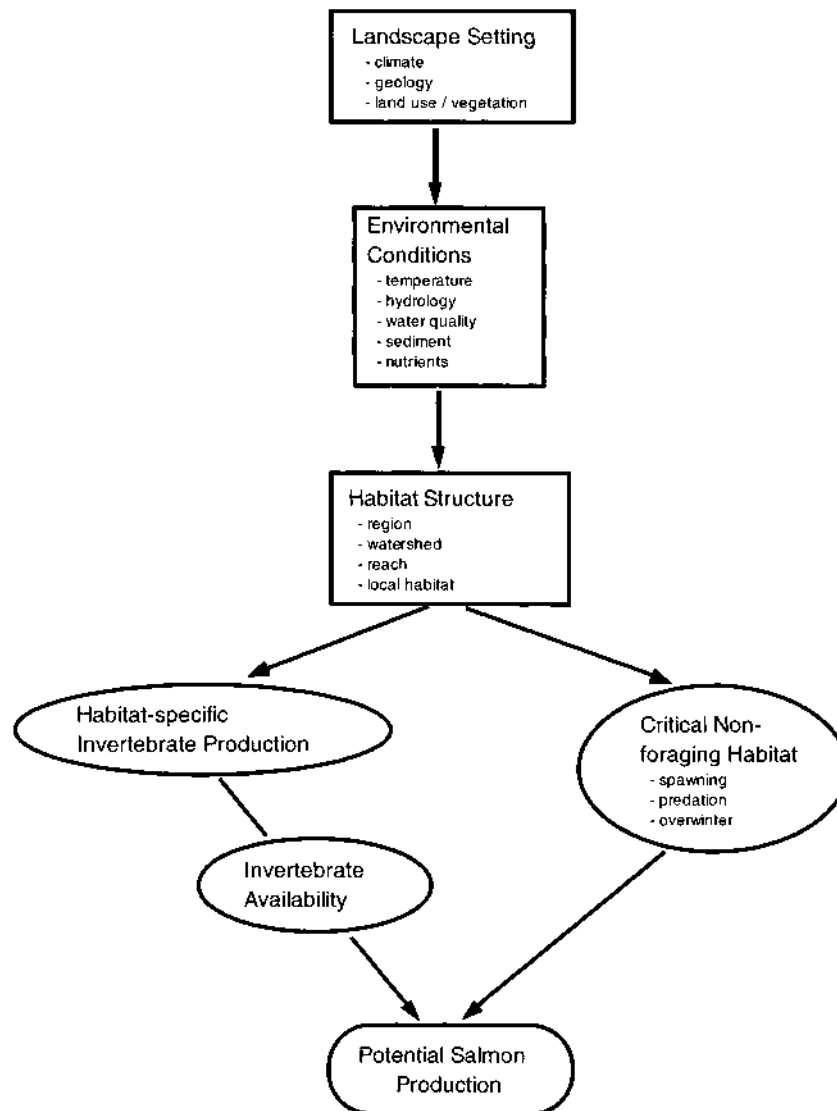
The freshwater phase of the Atlantic salmon (*Salmo salar*) life cycle is a critical period in which reproduction, early

growth, and survivorship set limits to production. Between spawning and smolt outmigration, production of young salmon depends on at least three broad environmental factors: an adequate food supply, suitable physical habitat, and

Received December 3, 1997. Accepted October 29, 1998. J14333

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**Fig. 1.** Conceptual overview of multi-scale, landscape framework for secondary production.

favorable physicochemical conditions. Juvenile salmon production can be limited by any one of these factors, a fact long appreciated (e.g., Lindroth 1965; Chapman 1966a). However, their relative importance is poorly understood, as is the extent to which they may interact to limit salmon production or change geographically in response to landscape and climatic features. A better understanding of these factors and their interactions is needed to facilitate the conservation, restoration, and management of Atlantic salmon.

Production is an integrated response to constraints and opportunities posed by abiotic and biotic processes and conditions that occur at a variety of spatial and temporal scales. Accordingly, production provides a comprehensive measure of ecological performance. Identifying spatial and temporal scales at which factors limiting production are most effectively expressed should improve our understanding of landscape variation in Atlantic salmon production. The hierarchical conception of stream habitat (e.g., Frissell et al. 1986) is most suitable for this task because it provides a multi-scale framework for assessing factors operating at different scales, ranging from local habitat to whole watersheds

to geographic regions. By calling attention to multiple constraints and processes, a multi-scale framework provides a general and realistic approach for the examination of ecological patterns (e.g., Imhof et al. 1996; Rabeni and Sowa 1996; Richards et al. 1996; Poff 1997). A better understanding of multi-scale constraints on Atlantic salmon production will allow us to better define the productive capacity of present populations and better identify areas where conditions could support viable salmon populations in the future.

In this paper, we consider how environmental conditions, habitat features, and invertebrate production limit salmon production in a multi-scale context (Fig. 1). Habitat and environmental conditions may directly limit salmon production by influencing survivorship, or they may indirectly limit salmon production by influencing prey production and availability. Because invertebrate production represents the transformation of a stream's energy base to a form available to juvenile salmon, consideration of different pathways providing support for invertebrate production in salmon nursery streams is necessary before fundamental factors that may limit salmon production can be identified. Although obvi-

ously not the only factor limiting salmon production, we pay particular attention to invertebrate prey production, because knowledge of this factor will allow guesses about maximum potential production of juvenile salmon (Richardson 1993). Despite the importance of prey production in determining salmon production, knowledge about this critical aspect of salmonid ecology in general, and Atlantic salmon ecology in particular, is surprisingly obscure (Waters 1993; Richardson 1993; Huryn 1996).

## Secondary production

In its broadest sense, "secondary production" refers to the formation of heterotrophic biomass over time (Benke 1993). Annual secondary production for a population of juvenile Atlantic salmon inhabiting a specific nursery stream, for example, will be the sum of all biomass produced by that population during a 1-year period (e.g.,  $g \cdot m^{-2} \cdot year^{-1}$ ). This summed production will include the new biomass actually remaining at the end of the year and all losses that occurred during that year. Losses may include mortality (disease, cannibalism, predation), loss of tissue reserves (starvation and mucous production), and emigration. Secondary production thus clearly differs from other measures commonly used to indicate the productivity of salmon nursery streams. "Smolt production," for example, refers to the number of smolt that leave a given nursery stream (e.g.,  $smolt \cdot area^{-1} \cdot time^{-1}$ ; Meister 1962; Mills 1989; Power and Power 1992). Although of obvious importance for management concerns, indicators such as smolt production do not necessarily provide information about the actual energy base of a given stream or how this energy is apportioned among different functional and trophic pathways.

Measurement of secondary production, at minimum, requires information about growth rate and biomass for the target population. Growth rate can be measured either directly from marked or confined individuals (invertebrates, fish), or as a function of size-at-age as indicated directly by growth rings deposited in bony structures (fish) or indirectly by population size structure (invertebrates, fish). The numerous methods for directly estimating secondary production are summarized in the excellent reviews by Bagenal (1978) and Benke (1984; 1993). Obtaining estimates of production for fish populations in small streams is relatively easy. For their invertebrate prey, however, such is not the case, due both to the large number of samples required for reasonably precise estimates of biomass in systems that are notoriously variable in space and time, and to difficulties in removing cryptic invertebrates from samples. Further, estimates of invertebrate secondary production for *entire stream communities* must be composites of measurements conducted separately for numerous species of consumers that may differ markedly in life histories and habitat distribution. Because of these difficulties, there are relatively few whole system estimates of macroinvertebrate production in streams and rivers (~40 streams; Benke 1993), even fewer for salmonid streams (~12 streams; Waters 1988; Huryn 1996). To our knowledge, there are no estimates for streams that currently support populations of Atlantic salmon; however, estimates do exist for two tributaries of the Connecticut River (Massachusetts) that probably contained populations of Atlantic

salmon early in the nineteenth century (Fisher 1977; Neves 1979).

Given the high labor costs required to directly measure invertebrate production, shortcut approaches are needed. Of the several offered (Benke 1984; 1993), two seem to hold reasonable promise. The first is based on the annual biomass turnover rate (annual production/mean annual biomass), or "P/B," which is a rough estimator of the average annual instantaneous growth rate for the target population. Waters (1969) showed that the P/B for cohorts within populations of invertebrates fell within a relatively narrow range (2–8), and suggested that *cohort production* might be estimated as the product of biomass and a suitable P/B (5 is usually suggested). When entire benthic communities are considered, however, the range of P/Bs for *annual production* varies from <1 to 117 because cohorts of different taxa may require periods of several weeks to several years (Benke 1993). The range of expected annual P/Bs can be narrowed by considering only small temperate streams (e.g., mean discharge ~0.1 to 1.0  $m^3 \cdot s^{-1}$  and mean annual temperature 5–10°C), where annual P/Bs range from 2.2 to 8.7 (10 streams) or from 4.2 to 7.9 (7 streams) (Benke 1993). The P/B approach for estimating production also has applications for fish as well as invertebrates. The P/B for populations of brown trout (*S. trutta*), for example, can be accurately estimated as a function of age structure (Waters 1992; see also Kwak and Waters 1997).

The second genre of promising shortcut approaches is the development of multiple regression models that estimate invertebrate production as a function of more readily measured variables, usually temperature, population biomass, and maximum body size (Morin and Bourassa 1992; Benke 1993; Morin and Dumont 1994; Benke et al. 1997). Similar equations are available for stream fish populations (e.g., Randall et al. 1995). The potential for estimating annual production of juvenile Atlantic salmon as a function of standing stock biomass, either mean annual or measured at a specific time of the year, is apparent from plots provided by Gee et al. (1978) and Randall and Paim (1982). The empirical approach has been criticized because it is prone to imprecision and inaccuracy, particularly when used to estimate production for single species at a single location (Benke 1993). However, the estimation of production for entire communities or groups of species (e.g., functional groups) as summed composites of estimates for single populations may increase the accuracy of this method (Benke et al. 1997). Indeed, using a variation of the regression approach, Benke (1993) and Webster et al. (1995) showed that production of invertebrate functional feeding groups (*sensu* Cummins 1973) may be estimated as various linear and polynomial functions of stream size (as indicated by mean annual discharge). These equations are particularly compelling because they may allow invertebrate production to be partitioned into categories of prey that differ in availability and quality (e.g., assimilability) for salmonids (cf. Wootton et al. 1996; Rader 1997), show different levels of dependence of secondary production on riparian and watershed energy and nutrient sources (Doucett et al. 1996), and follow patterns that may change with stream size in predictable ways (Vannote et al. 1980). The testing and refinement of the application of such empirical approaches for estimating secondary production merits fur-

ther research because they may be particularly useful for estimating biologically reasonable ranges of production at large spatial scales required for multi-scale studies of stream ecosystem processes (e.g., among general categories of streams).

### Evidence for food-limitation of salmonid production

Published research on stream salmonids suggests that limitation of Atlantic salmon production by invertebrate production cannot be easily dismissed, especially in nutrient-poor waters (see Richardson 1993). Several studies have shown positive correlations between food abundance in streams and salmonid growth rates (Wilzbach et al. 1986; Erkinaro and Niemela 1995), biomass (Murphy et al. 1981; Bowlby and Roff 1986b) and abundance (Slaney and Northcote 1974). Experimental support for food-limitation of fish in salmonid streams also exists. In an early study, Mason (1976) amended food supply to juvenile coho salmon (*Oncorhynchus kisutch*) in British Columbia headwater streams and observed an increase in growth rates and lipid storage. Peterson et al. (1993) used stable isotope analysis to show that the addition of inorganic fertilizer to an oligotrophic Alaskan river resulted in rapid increases in benthic algal and insect production; within 3 years, increased growth rates of young-of-year and adult grayling (*Thymallus arcticus*) were attributed directly to enhanced algal production. Similarly, in a forested British Columbia stream, nutrient addition stimulated primary productivity and increased the weights of two species of salmonid fry (Johnston et al. 1990).

In Atlantic salmon streams, however, there is mixed evidence for food limitation. Studies showing a positive relationship between prey abundance and salmon biomass (e.g., Egglisshaw 1967; Gibson and Galbraith 1975; Gibson and Dickson 1984), and density-dependent growth cohorts of Atlantic salmon in Norway (Bergheim and Hesthagen 1990; Heggenes and Borgstrom 1991) suggest that food limitation can occur. In addition, Erkinaro and Niemela (1995) showed that high growth rates of Atlantic salmon among tributaries of a Finland stream system were related with high levels of drifting prey. By contrast, however, a 10-year study of juvenile Atlantic salmon production in the Miramichi and Restigouche rivers (New Brunswick) showed that annual variation in growth rate was minimal and independent of fish abundance (Randall and Chadwick 1986). Production was most closely related to population abundance and biomass rather than growth rate. Since food limitation was clearly not a factor in determining production, Randall and Chadwick (1986) suggested that non-trophic factors that influenced recruitment — overfishing of adult salmon was specified — controlled abundance and maintained juvenile salmon production below carrying capacity. Gee et al. (1978) similarly reported that production of Atlantic salmon in the River Wye (Wales) was controlled by spawning success rather than prey availability.

### Guesses about trophic support for juvenile Atlantic salmon

Waters (1988) reviewed studies of salmonid — invertebrate production relationships worldwide to show that maximum

levels of annual production by populations of stream dwelling salmonids (primarily brown trout) ranged to 36 g wet mass (WM) · m<sup>-2</sup>, with levels >10 g WM · m<sup>-2</sup> indicating “productive” streams. Similar data for populations of juvenile Atlantic salmon, however, are scarce. Randall and Chadwick (1986) summarized production data for seven streams around the North Atlantic to show that mean annual production ranges from <1 to about 9 g WM · m<sup>-2</sup>. The maximum levels of annual production yet reported are 16–17 g WM · m<sup>-2</sup> (Mann 1971; Bergheim and Hesthagen 1990). It is clear that production by juvenile Atlantic salmon can attain levels expected for productive trout streams.

Wet mass can be converted to ash-free dry mass (AFDM), which is more easily used for comparisons, using conversion factors provided by Waters (1988). The mean annual production of 8.9 g WM · m<sup>-2</sup> reported for Atlantic salmon in the Shelligan Burn (Egglisshaw and Shackley 1977), for example, is roughly equivalent to 1.6 g AFDM · m<sup>-2</sup> · year<sup>-1</sup>. Based on a food conversion efficiency of 0.2 for salmonids (Waters 1988), 1.6 g AFDM of annual salmon production will require roughly 8.0 g AFDM · m<sup>-2</sup> of annual prey production with 100% utilization.

Egglisshaw (1970) reported that the mean standing stock of benthic fauna in the Shelligan Burn measured during a single year (1962–1963) was 2.9 g dry mass (DM) · m<sup>-2</sup> (roughly equivalent to 2.6 g AFDM · m<sup>-2</sup>). Egglisshaw and Shackley (1985) later reported a standing stock of 1.2 g DM · m<sup>-2</sup> (~1.1 g AFDM · m<sup>-2</sup>), a value presumably based on a survey conducted in 1969–1970 (Egglisshaw and Shackley 1977). Assuming that the mean of these values estimates the expected standing stock of prey during the study, the turnover rate required to provide prey production that matches the estimated consumption is 4.2 (=8.0/1.9). This turnover rate is clearly realistic, given that turnover rates as high as seven are not unexpected for benthic invertebrate communities in temperate streams similar in size (mean discharge = 0.12 m<sup>3</sup> · s<sup>-1</sup>) and mean temperature (~7°C) (Benke 1993).

Atlantic salmon are not the only species of fish in the Shelligan Burn, however. There are also populations of brown trout and eels (Egglisshaw and Shackley 1977). The combined mean annual production of brown trout and Atlantic salmon during the study was 19.2 g WM · m<sup>-2</sup> (~3.5 g AFDM · m<sup>-2</sup>; eel production was not measured). The turnover rate of benthic invertebrate biomass required to support this combined production is roughly 9.2. This turnover rate is unreasonably high (Benke 1993). The preceding calculations are based on the assumption that both trout and salmon feed exclusively on benthic invertebrates. Egglisshaw (1970), however, reports that terrestrial invertebrate prey may comprise ~30% of total prey consumption by brown trout, and ~23% for Atlantic salmon in the Shelligan Burn. Assuming that consumption of terrestrial prey is only 20%, the turnover rate of benthic prey required to meet the demands of both trout and salmon is 7.4. Although in the high range expected for streams similar to the Shelligan Burn, this turnover rate is clearly realistic (cf. Benke 1993), and is similar to the turnover rate of 7.1 to 7.4 reported by Neves (1979) for macroinvertebrates associated with cobble habitat in what was presumably an historical Atlantic salmon stream in New England.

A probable maximum amount of invertebrate prey production expected for salmon streams can be determined, using a summary table provided by Benke (1993). Streams with a mean annual temperature  $\leq 8.5^{\circ}\text{C}$  and mean annual discharge  $\leq 1 \text{ m}^3 \cdot \text{s}^{-1}$ , and without significant organic pollution, are expected to have levels of invertebrate production ranging from about 4 to 24 g AFDM  $\cdot \text{m}^{-2} \cdot \text{year}^{-1}$ , with values  $\leq 8 \text{ g AFDM} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$  being most common (7 out of 9 reports, Benke 1993). Assuming a 20% energetic efficiency (Waters 1988), and assuming that no prey production is lost to pathways other than salmon predation, the maximum salmon production expected for nursery streams will range from about 0.8 to 4.8 g AFDM  $\cdot \text{m}^{-2} \cdot \text{year}^{-1}$  (=6 to 22 g WM), with levels of about 1.6 g AFDM  $\cdot \text{m}^{-2} \cdot \text{year}^{-1}$  (=8.9 g WM) the most reasonable maximum expected level. These estimates reflect reported literature values of annual salmon production that range from  $<1$  to about 9 g WM  $\cdot \text{m}^{-2}$ , with an extreme maximum of 17 g WM  $\cdot \text{m}^{-2}$  (Mann 1971; Randall and Chadwick 1986).

On the basis of these admittedly "back of the envelope" calculations and sparse data, it appears that the higher ranges of production reported for Atlantic salmon streams may be accommodated by reasonable levels of benthic prey production. However, it should also be noted that production by predatory invertebrates and other fish will also require some of the benthic prey production which will reduce that available to salmon. Accordingly, since it appears that a significant proportion of prey production may at times be required to support juvenile salmon production, the potential for the coupling of these two compartments can be strong. Terrestrial invertebrates may also provide an important subsidy to the diet of juvenile salmon that will reduce pressure on benthic prey, yet the quantitative significance of terrestrial invertebrates as a source of food for salmon is poorly understood. Finally, it should be noted that over the 10-year period that Atlantic salmon production was measured in the Shelligan Burn, annual production ranged more than two-fold (5.5 to 12.1 g WM  $\cdot \text{m}^{-2}$ ; Egglisshaw and Shackley 1977). Factors underlying such long-term temporal variation must be identified before a predictive knowledge about the interrelationship between production of Atlantic salmon and their prey can be attained.

### Is "invertebrate production" equivalent to "prey production" for juvenile Atlantic salmon?

#### *Benthic prey*

Juvenile Atlantic salmon are opportunistic foragers, able to switch between benthic and drift feeding depending on relative abundance of preferred prey (e.g., Gibson 1993). Recent experimental work, however, indicates that salmon parr spend a majority of their time feeding directly from the drift, even when drift availability is locally reduced (Nislow et al. 1998). Therefore, it would appear that juvenile salmon acquire much (if not most) of their energy by drift feeding, and factors that reduce the availability of drifting invertebrates to salmon may present a bottleneck to salmonid production.

Benthic invertebrates have different tendencies to drift and are thus differentially available to drift-feeding salmonids (Waters 1972). Compared to species that are common

components of drift, those that do not drift frequently will be less available to salmonids, either because they are cryptic (e.g., some cased caddisflies) or because they are inaccessible (e.g., interstitial fauna). Recent work showing competitive suppression of palatable, drifting prey by invulnerable prey (Power et al. 1996; Wootton et al. 1996) indicates that estimates of gross invertebrate production alone may not be sufficient to understand limits on salmon production; consideration of community composition and relative availability of potential prey may also be required. If this is the case, then a functional approach that characterizes the availability of invertebrate guilds to drift-feeding salmonids would be valuable. Ideally, guilds should be defined to satisfy two conditions: (1) differential availability to salmon predators (to translate benthic production to potential salmon production), and (2) differential sensitivity to environmental conditions (to understand landscape variation in conditions that constrain invertebrate guild availability).

The ecological implications of differential availability have recently been examined by Rader (1997), who classified 95 benthic invertebrate taxa in the central Rocky Mountain region (U.S.A.) into availability guilds for drift-feeding salmonids. He used a number of behavioral and microhabitat preference characteristics that are likely to influence drift entry (e.g., mobility, exposure to flow, body size). When ranked according to availability, the taxa showed significant correlations with the actual ranks of invertebrates in trout stomach contents as reported in three published studies. The most available taxa included the mayfly *Baetis*, blackfly (Simuliidae) larvae, and amphipods, all widely distributed and known as "drifters" (e.g., Waters 1972). The most unavailable taxa consisted mostly of species occupying hyporheic or depositional habitats (including burrowing species). Taxa with intermediate availability occurred in erosional areas, but were not generally found in microhabitats fully exposed to flowing water. In general, species that actively swim or drift and reside in flow-exposed microhabitats (e.g., *Baetis* and simuliids) are most available to drift-feeding salmonids. These findings imply that, all other factors being equal, Atlantic salmon production should be greater in streams having high relative production of these drifting invertebrate species.

#### *Terrestrial prey*

Terrestrial invertebrates may at times be important sources of food for stream fishes in general (Chapman 1966b; Hunt 1975; Waters 1993), and juvenile Atlantic salmon in particular (Egglisshaw 1970; Gibson and Cunjak 1986). Terrestrial invertebrates, for example, have been shown to be important prey for juvenile Atlantic salmon in Scotland and Newfoundland (Egglisshaw 1970; Gibson and Cunjak 1986), and they are almost certainly important across the Atlantic salmon's entire range. These studies indicated that terrestrial invertebrates may at times compose  $>20\%$  of the stomach content. Such reports, however, tend to obscure how seasonal patterns of the relative availability of prey in salmon streams may magnify the importance of terrestrial sources of prey to salmon survival. In heavily forested, oligotrophic streams, in particular, the life cycles of many invertebrate species are synchronized with the input of leaf detritus during the autumn. Growth occurs during autumn and spring,

with adult insects emerging in late spring and early summer. As a result, the biomass of benthic invertebrate prey may be at its lowest point during summer, when metabolism of salmon is maximal due to summer water temperatures (Hynes 1970; Hunt 1975; Cada et al. 1987; Garman and Moring 1993). The summer period may represent an energetic "bottleneck," and the importance of terrestrial invertebrates to the survival of juvenile salmon may be much greater than indicated by quantitative considerations of stomach content alone. Mason (1976) supported this view by showing that growth and survival of coho salmon in British Columbia was food-limited during the summer months, and that salmon size and density were increased several fold by experimental feeding. If a similar relationship occurs in Atlantic salmon streams, riparian inputs of terrestrial invertebrates have clear implications for management of salmon streams for maximum salmon production. This aspect of Atlantic salmon ecology is poorly understood.

### **A multi-scale framework for considering prey and Atlantic salmon production in streams**

#### **The importance of scale**

Consideration of multi-scale constraints on ecosystem structure and function is an area of growing interest in stream ecology (e.g., Frissell et al. 1986; Rabeni and Sowa 1996; Poff 1997), and we suggest that a multi-scale perspective will be useful in assessing and predicting variation in Atlantic salmon production across the diverse landscapes that comprise its range. The physical structure of streams can be conveniently defined using a hierarchy of spatial scales (e.g., Frissell et al. 1986). Because environmental factors that limit either prey production or non-trophic habitat needs of Atlantic salmon operate at different scales, a focus on only one scale may result in a failure to identify limiting factors associated with another scale (see Rabeni and Sowa 1996).

Over its life span, the highly mobile, anadromous Atlantic salmon clearly experiences environmental and ecological factors occurring over a wide range of spatial and temporal scales (Folt et al. 1998). We focus on four of what we consider to be critical hierarchical spatial scales and then consider how selection of a particular scale of observation may influence perceptions of the importance of different factors that control Atlantic salmon production. Where possible, we also consider how these factors vary at different temporal scales, because temporal variability is a critical structuring force in running water ecosystems (Resh et al. 1988; Poff and Ward 1989, 1990; Townsend and Hildrew 1994; Poff et al. 1997).

#### **The habitat hierarchy**

##### *Regional scale*

At the regional scale, climate and biogeography are the most important factors that may regulate salmonid production. Climate determines thermal regime, amount and timing of runoff, and vegetation potential. Across the range of Atlantic salmon, clear regional differences in these climatic factors are evident (see Elliott et al. 1998). More northerly

streams tend to have longer winters with extensive ice cover, and shorter, cooler summers than more southerly or northern maritime streams. The scouring effects of catastrophic ice breakup, for example, will be more pronounced in northern streams. Southern streams may have potential for higher invertebrate and salmon production because of a longer growing season. Warmer summer temperatures, however, may directly limit the growth potential of salmonids. Southern streams will also tend to have relatively less late-spring and summer discharge because of less precipitation storage as snow.

The role of biogeography in determining levels of production at the regional scale has received very little attention. The correlation between benthic invertebrate community composition and regional patterns of vegetation is well known (Ross 1963; Cummins et al. 1989); however, the influence that this relationship has on Atlantic salmon throughout a broad region that includes temperate hardwood forests, boreal coniferous forests, and taiga is unknown. Assuming that growth of juvenile Atlantic salmon is prey limited at times, regional factors that have strong bearing on food quality and quantity for invertebrates as well as the composition of prey communities may have subtle but probably significant effects on their production.

##### *Watershed scale*

Geology, vegetation cover, and land use are probably the major determinants of salmonid production at the watershed scale. Bedrock geology regulates the types and quantities of nutrients available for dissolution and also influences stream thermal regime. Streams draining watersheds with carbonate bedrock, for example, tend to have higher concentrations of dissolved ions and less variable thermal and hydrologic regimes, and support higher levels of total secondary production compared to streams draining other bedrock types (Krueger and Waters 1983; Huryn et al. 1995). Streams draining watersheds with deep glacial deposits also tend to have high thermal and hydrologic stability and may support higher levels of invertebrate production compared to streams draining watersheds with shallow soils (Krueger and Waters 1983). Watershed vegetation cover, land use and land-use history interact to influence secondary production in streams by numerous direct and indirect pathways, including hydrology, light, thermal regime, water chemistry, channel sediments and morphology (Freeman and Wallace 1984; O'Hop et al. 1985; Wallace and Gurtz 1986; Sallenave and Day 1991; Grubaugh and Wallace 1995; Sanchez and Hendricks 1997).

##### *Reach scale*

A stream reach is defined here as a length of stream channel that incorporates several local habitats. The distribution and abundance of local habitats are dictated by channel morphology and riparian conditions (Gregory et al. 1991). At the reach scale, stream width has long been identified as a central determinant of food quality and quantity, primarily because of its effect on the relative influence of riparian vegetation on stream energy budgets (Vannote et al. 1980). Habitat complexity also has important influences on reach-scale patterns of production by invertebrates (Huryn and Wallace 1987). Reaches that are constrained by bedrock will tend to

have reduced habitat complexity and hyporheic volume, and faster through-flow of organic matter and nutrients compared to unconstrained, alluvial reaches (Gregory et al. 1991). Such reaches are predicted to have high proportions of low-productivity habitat (e.g., bedrock run and glide) and lower levels of invertebrate and fish production compared to unconstrained reaches (e.g., alluvial cobble-riffle). This relationship is poorly defined, however, and may become inverted, for invertebrates at least, in bedrock-constrained reaches with an abundant cover of aquatic mosses (Grubaugh et al. 1997). Reaches that are separated by selective barriers to fish movements, such as waterfalls or beaver dams, may show differences in fish community structure (Crowl et al. 1992; Schlosser 1995) that may effect levels of reach productivity because of cascading effects within food webs (Huryn 1998).

#### *Local-habitat scale*

Water depth, velocity, and type of substratum are often used to identify spatially distinct channel features designated here as local habitats (or channel unit habitats — Hawkins et al. 1993). Local-habitat type, such as riffle or pool, strongly influences the local distribution and abundance of aquatic fauna, both invertebrates (Huryn and Wallace 1987) and fish (Angermeier 1987; Schlosser 1991). Secondary production in high-gradient headwater streams tends to be relatively uniform among habitats, largely because of high levels of production in debris-dam pools (Huryn and Wallace 1987). In lower gradient streams with more mobile beds, however, riffle habitats are usually considerably more productive than pools (Fisher 1977; Bowlby and Roff 1986a; Grubaugh et al. 1997). Not only can habitat influence the production of prey biomass, but by influencing their community structure, this factor can also influence the relative availability of quality prey to drift feeding salmonids (Rader 1997).

#### **Factors that determine prey production in Atlantic salmon streams**

Secondary production is essentially the product of the growth rate and biomass of an animal population, and the numerous factors that determine production will generally operate upon these variables. There are available a number of excellent reviews of factors affecting growth and production of stream invertebrates (Resh and Rosenberg 1984; Benke 1993). Rather than providing a comprehensive treatment of all factors identified as significant in this regard, we attempt to highlight factors that may be significant for Atlantic salmon streams in particular.

#### *Temperature*

Temperature directly regulates rates of metabolism, growth, and development in stream invertebrates (Sweeney 1984). Atlantic salmon streams are largely restricted to the boreal or sub-boreal biomes, which are characterized by short summers and long, cold winters. Accordingly, P/B ratios are expected to be low in Atlantic salmon streams, due both to the short length of the growing season and to the relative dominance in these streams of invertebrate species that generally do not produce more than one generation per year (Clifford 1982; Jacobi and Benke 1991). At the watershed scale, bedrock geology, vegetative cover, and land use influ-

ence thermal regime, by regulating soil temperatures and the degree to which precipitation infiltrates into the soil and moves as groundwater to the stream. Large contributions of groundwater to stream discharge, for example, will moderate thermal extremes by buffering against cold winter conditions in northern regions or warm summer conditions in southern regions of the Atlantic salmon's range. Large-scale removal of forest cover due to clear cutting or row cropping, on the other hand, will enhance thermal extremes because of its effect on temperatures of soil and infiltrating precipitation. Thermal regimes are also influenced by reach-scale features, such as riparian cover or the relative proportion of deep pools that reduce rates of heat exchange with the atmosphere. Finally, variation in thermal regime among local habitats has been shown to influence spatial patterns of invertebrate growth rates and may therefore have consequences for prey production (Gresens 1997).

#### *Food*

Invertebrate growth rates are strongly influenced by food quality (Hill 1992) and quantity (Richardson 1991). The quality of food type is determined both directly and indirectly by vegetation cover, and this has important effects on the structure of prey communities for Atlantic salmon. The quality, quantity, and timing of input of terrestrial detritus to streams may vary considerably in quality at regional scales across the range of the Atlantic salmon (e.g., hardwood detritus in the south, softwood detritus in the north), with this variability being reflected by differences in community structure, life histories and probably production dynamics of resident macroinvertebrate populations (Ross 1963; Cummins et al. 1989). Latitudinal trends in vegetation will also effect water chemistry, with acidic streams — often characterized by low levels of invertebrate production (Krueger and Waters 1983) — being more widespread at higher latitudes. At more local scales, e.g., in locations approaching or exceeding the timberline (either high altitude or high latitude), or in wide and shallow rivers, the absence of canopy-forming vegetation may produce a change in primary energy source, from terrestrial detritus to algae, which will be correlated with changes in macroinvertebrate community structure and production (Wiggins and Mackay 1978; Vannote et al. 1980; Behmer and Hawkins 1986). Nutrient concentrations are also important determinants of food quality and quantity and will vary widely throughout the range of the Atlantic salmon depending on regional geology and watershed land-use. Limited information indicates that moderate levels of agricultural land-use actually enhance Atlantic salmon production because of associated inputs of nutrients to otherwise oligotrophic streams in Europe (Kennedy et al. 1983; Bergheim and Hesthagen 1990). Presumably this increase is due to bottom-up control of prey production (cf. Johnston et al. 1990; Peterson et al. 1993).

#### *Disturbance*

Although poorly studied, the effects of winter freezing and subsequent ice breakup on aquatic invertebrate production are probably particularly important regional-scale factors influencing the productivity of Atlantic salmon streams. Ice breakup and associated flooding, which has been shown to cause large increases of drifting insects and detritus in



northern rivers, are likely a critical determinant of annual patterns of prey biomass and species composition (Hudon 1994). The effect on invertebrate production dynamics of floods not associated with ice breakup will be a function of hydrologic regime and substratum stability (Scarsbrook and Townsend 1993). The timing and frequency of floods relative to life cycle stage of the invertebrates (e.g., winter or summer, cf. Hudon 1994; Huryn et al. 1995) and the presence of channel refugia during floods (Scarsbrook and Townsend 1993; Palmer et al. 1996) can influence magnitude of biomass loss. Regional differences in climate and watershed or reach differences in sediment size and mobility will interact to influence the local importance of disturbance in any particular Atlantic salmon stream. In general, however, the fact that many invertebrates in north temperate and boreal streams require at least 1 year to complete their life cycles implies that recovery of biomass due to scouring floods will be slow, especially when contrasted with streams in regions having communities of invertebrates characterized by rapid growth rates and short life cycles (e.g., Fisher and Gray 1983). Accordingly, the reduction of invertebrate biomass by scouring floods, especially those associated with ice breakup (Hudon 1994), implies reduced food supply for Atlantic salmon on an annual scale. Understanding the effects of ice breakup is probably crucial to understanding long-term variability of production dynamics in Atlantic salmon streams.

#### *Biotic interactions*

Although poorly studied, regional invertebrate-species pools may influence the proportion of total prey production readily available to salmon. Wootton et al. (1996), for example, observed that the abundances of palatable prey species in California streams that support high growth rates in juvenile steelhead trout (*O. mykiss*) can be reduced by the presence of a caddisfly species (*Dicosmoecus*) that is invulnerable to predation. *Dicosmoecus*, along with other invulnerable invertebrates (e.g., aquatic moth larvae), tends to dominate in drought years when scouring floods are rare (Power 1992), suggesting that interannual variation in climate may indirectly influence production by steelhead trout via production dynamics of prey communities. The extent to which regional differences in dominant, invulnerable species may influence prey availability to Atlantic salmon (or other stream predators) and thus potentially limit salmon production is virtually unknown.

Regional patterns of the composition of fish assemblages may also have consequences for production by their invertebrate prey. Some invertivorous fish species, for example, may depress prey production directly by reducing prey biomass more effectively than others (Huryn 1998) or indirectly by affecting invertebrate feeding behavior (see below). Because of these differences in feeding behavior, different assemblages of fish will probably have different effects on their prey populations. Studies of how biogeography controls community interactions, and how these interactions may function to regulate secondary production over large areas will enhance understanding of factors contributing to variation in Atlantic salmon production at the regional scale.

On the local habitat-scale, interspecific competition (Hill 1992) and the non-lethal effects of predators (McPeck and

Peckarsky 1998) have been shown to result in a decline in invertebrate growth rates. The effects of this latter factor are currently receiving a great deal of attention because, although subtle, they are clearly widespread and of substantive quantitative significance (McPeck and Peckarsky 1998). This is because avoidance behavior by benthic insects in response to their salmonid predators usually results in a reduction in time spent feeding, which may have consequences for rates of larval growth and development as well as fecundity of adults (Ball and Baker 1996; McPeck and Peckarsky 1998). A reduction in growth or feeding activity may ultimately affect levels of secondary production by prey populations and primary producers, which in turn may influence production dynamics of adjacent trophic levels (Flecker and Townsend 1994; McIntosh and Townsend 1995; 1996; Peckarsky and McIntosh 1998). It is important to note that although avoidance behavior by invertebrates operates at a relatively local scale (e.g., local habitat), factors that affect the distribution of their salmonid predators are probably controlled by factors operating at the reach, watershed, or regional scale (e.g., Crowl et al. 1992).

#### *Terrestrial invertebrates*

Although there have been many studies demonstrating that terrestrial invertebrates are consumed by stream fishes, only a handful have attempted to directly quantify the importance of this food source to fish production or to determine factors that influence quantities of terrestrial invertebrates that enter streams (Nelson 1965; Mason and Macdonald 1982; Edwards and Huryn 1995, 1996; Huryn 1996; Cloe and Garman 1996; Wipfli 1997). The most recent research has answered questions about how different riparian management activities influence terrestrial inputs to streams (Edwards and Huryn 1996) and how riparian zones might be modified to enhance this food source (Wipfli 1997). Edwards and Huryn (1996), for example, showed that salmonid streams in New Zealand with riparian zones with either forest or native grasses received significantly greater amounts of terrestrial invertebrates compared to streams bordered by pasture. Wipfli (1997) found that the species composition and successional stage of riparian vegetation along forested streams in Alaska can influence the availability of terrestrial invertebrates to juvenile coho salmon.

#### **Non-trophic constraints on Atlantic salmon production**

Close coupling between Atlantic salmon and prey production is not expected if factors other than prey production and availability have strong effects on salmonid growth or mortality (e.g., Gibson et al. 1993; Gotceitas and Godin 1993). The potential impact of such "non-trophic factors" on any particular population of Atlantic salmon, however, will depend on the availability of specific habitat types that promote growth and minimize mortality over the freshwater period of the salmon life cycle. Here, we briefly consider a number of non-foraging habitat types thought to be critical to Atlantic salmon production. Assessment of the relative importance and how the availability of these critical habitats may change across the range of Atlantic salmon is necessary for understanding spatial variation in Atlantic salmon production.



### *Spawning and summer feeding habitat*

Adult salmon construct redds in small streams providing erosional areas with moderate velocities and depths and with unarmored and porous substrata (see Gibson 1993). Lack of available spawning habitat (at the local-habitat, reach, or watershed scale) will obviously limit salmon production (see Gee et al. 1978). After emergence from the redd, fry generally disperse but remain within riffles to forage during the spring and summer. Some age-class segregation among parr occurs because, as juveniles grow, they tend to move into slightly deeper, faster water with coarse substrata.

Atlantic salmon generally require water temperatures  $<20^{\circ}\text{C}$  for positive growth. In more southerly latitudes, these temperatures may be exceeded during summer. Gibson (1988) observed juvenile salmon in pools but not riffles at temperatures of  $24^{\circ}\text{C}$ , suggesting reduced growth potential. In some streams, groundwater sources may be a critical factor in maintaining suitable thermal habitat for salmonids (cf. Meisner et al. 1988). Indeed, survival of juvenile salmon in a Maine river has been positively associated with summer discharge. Adequate levels of discharge are apparently required to maintain both cooler temperatures and available feeding habitat (Havey and Davis 1970).

### *Overwintering habitat*

As water temperatures cool in the autumn, juvenile salmon move into sheltered habitats to overwinter. Parr may hide under large substrata in runs and riffles (Gibson 1978; Cunjak 1988), or to move into deep pools (Allen 1940; Jensen and Johnsen 1986), or show both behaviors (Cunjak 1996). The availability of sheltered winter habitat is probably most critical in streams with extensive ice cover, which reduces total habitat volume and can cause high parr mortality during ice breakup. Mortality risk may vary with reach-scale habitat structure and from year-to-year. For example, in years when ice breakup occurs slowly, stream riffles tend to be more heavily scoured than pools; however, in years of dynamic, rapid breakup, all habitat types tend to be scoured (R.A. Cunjak, Dept. Fish. and Oceans, personal communication). In some watersheds, local groundwater inflows may serve to maintain important open-water refuges during winter (Cunjak 1996). The potential significance of winter conditions to production is revealed in comparative studies. Randall and Paim (1982) reported that salmon production tended to be lowest in streams where ice cover and near  $0^{\circ}\text{C}$  temperatures occur for about 6 months every year (e.g., New Brunswick, northern Norway). The highest levels of production were recorded from streams where near-zero temperatures occur for  $<2$  months of the year (e.g., Egglishaw 1970). These differences were attributed to lower biomass and, to a lesser extent, slower rates of growth in the colder streams (Randall and Paim 1982). This conclusion suggests that biomass losses caused by winter mortality should be suspected as an important mechanism controlling patterns of production at watershed and regional scales.

### *Refugia from predation and competition*

Although juvenile salmon apparently prefer riffle habitat in the summer, they may frequent pools when potential competitors and predators are absent. There is also some evidence that parr growth rates may actually be higher in pools

(see Gibson 1993). Whether avoidance of pools by parr is due to relatively poor competitive ability compared to other species (cf. Fausch 1998) or due to vigilance against potential predators (e.g., adult brown trout, kingfishers) is not known. It has been shown experimentally, however, that juvenile Atlantic salmon exposed to model rainbow trout or stuffed kingfishers show reduced foraging activity (Metcalf et al. 1987; Gotceitas and Godin 1993).

### *Refugia from high flow*

Spates may reduce salmon production through several mechanisms. Spates that occur prior to fry emergence can scour redds and cause egg or alevin mortality. This is probably of more concern in watersheds where some autumn and winter precipitation falls as rain (e.g., in southern end of range or coastal streams — see Elliott et al. 1998). Large rain-on-snow events can be particularly devastating if they cause redds to be scoured, as has been shown for fall-spawning salmonids in the California Sierra-Nevada (Erman et al. 1988). At the watershed scale, human activity that elevates sediment loads in streams may also increase the effective scour depth for a given discharge, thus reducing egg/alevin survival (Montgomery et al. 1996).

Spates that occur after dispersal from the redds can also cause mortality of young salmon. Juvenile fish in general are vulnerable to downstream displacement by floods (e.g., Harvey 1987). Environmental factors that mitigate mortality from floods include stable large woody-debris (Moore and Gregory 1988; Pearsons et al. 1992) or streambed structure that provides hydraulic dead zones during high water (Lancaster and Hildrew 1993).

## **Predicting invertebrate and Atlantic salmon production at multiple scales**

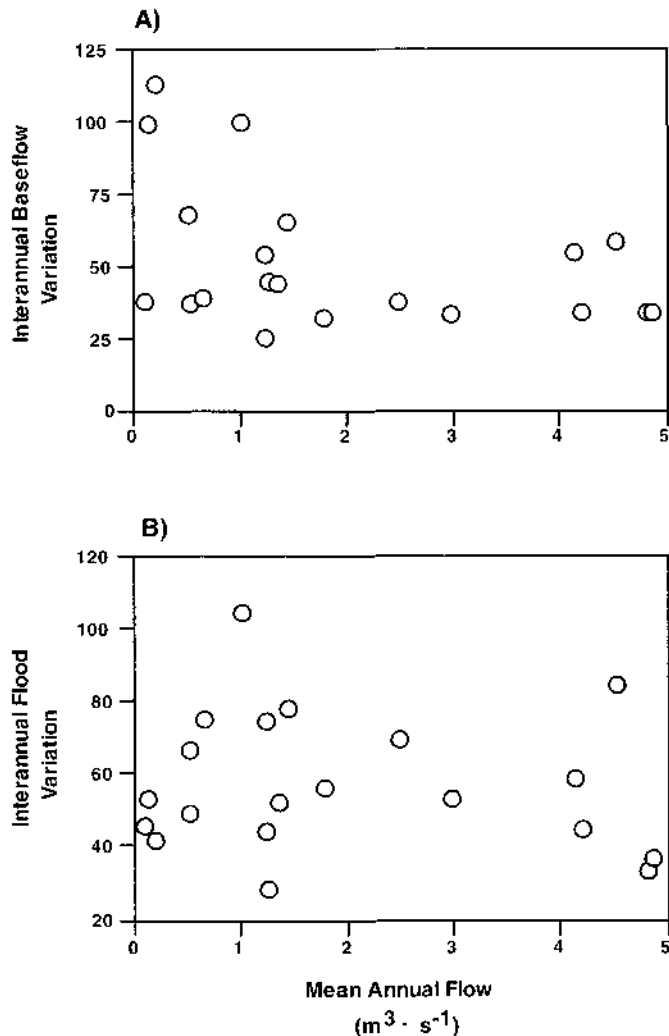
Clearly, the empirical data do not exist to allow us to rigorously demonstrate the details of how a multi-scale framework operates to control production of juvenile Atlantic salmon. Nonetheless, we believe an attempt to organize existing information in a hierarchical context will aid in identifying important knowledge strengths and gaps that suggest critical research areas that could help define limits to Atlantic salmon production across its enormous range. In keeping with the spirit of the workshop that spawned this paper, we attempt to make some predictions about expected patterns of invertebrate and salmon production at different habitat scales. We view these predictions as critical uncertainties, which, if answered, would greatly increase our understanding of fish-habitat relations and thus contribute to Atlantic salmon conservation, restoration, and management.

### **General prediction**

#### *Larger-scale factors can override factors controlling salmon production at smaller scales*

This general prediction is central to a hierarchical view of habitat constraints on ecosystem productivity. For example, water chemistry, water temperature, and sediment supply, important determinants of the biological characteristics of streams, are largely controlled by watershed-scale processes. These factors interact to exert strong control on habitat

**Fig. 2.** Relationship between stream size (mean annual flow) and (a) interannual baseflow variation (coefficient of variation in the ratio of annual low flow to mean annual flow) and (b) interannual flood variation (coefficient of variation in magnitude) for 20 unregulated streams in New England (U.S.A.).



complexity and stream productivity at the reach scale. Similarly, reach-scale factors, such as riparian conditions or channel width, influence productivity at the local habitat scale by regulating the supply of terrestrial vs. instream carbon sources. Understanding of watershed to local habitat-scale processes occurring within the range of the Atlantic salmon is crucial for effective restoration and management of streams because effort can then be focused on the hierarchical scale(s) that will provide the most effective response. Given the importance of the general prediction of top-down control within a habitat hierarchy, however, it is significant to note that some mitigation procedures, such as use of riparian buffer zones to reduce sediment or nutrient inputs to streams, are actually attempts to invert the habitat hierarchy by reducing the effect of a higher-order factor (e.g., watershed) by modifying a lower-order factor (e.g., reach). However, the efficacy of small-scale remediation in a setting of

larger-scale watershed perturbation may be limited (see Frissell and Nawa 1992; Roth et al. 1996; Allan et al. 1997).

### Watershed scale predictions

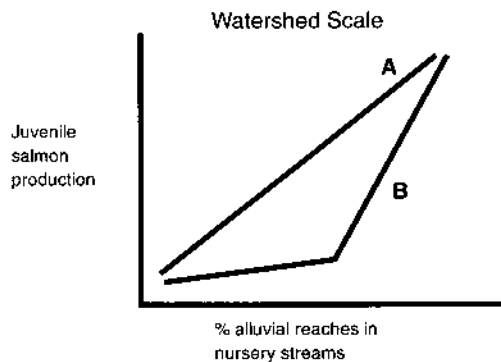
#### *Hydrologic regime will be a determinant of salmon production*

Hydrologic extremes, in particular, may serve as surrogates for habitat quantity and perhaps quality, and thus be useful in predicting differences in production among salmon streams (cf. Poff and Ward 1989). Streams with stable baseflows will have high relative thermal stability, to be less prone to drying, especially during summer, and to have a favorable chemistry (alkalinity, pH) that supports greater invertebrate and salmonid production (Krueger and Waters 1983; Kwak and Waters 1997). Figure 2a shows for 20 streams in New England, U.S.A. (from Poff 1996) that the interannual variability in baseflow stability (a measure of how low streamflow drops relative to the mean annual flow) varies substantially, especially for small streams  $< 2 m^3 \cdot s^{-1}$ . Providing that sediment supply is sufficient to maintain spawning habitat, streams with lower variability in baseflow stability may be expected to afford more favorable habitat for salmon production. In a similar vein, interannual variability in the magnitude of high water conditions may also indirectly assay risk to juvenile salmonids during the few to several years they reside in a nursery stream. For the same 20 small New England streams, the range of variability in high flow conditions varies by a factor of two, suggesting some streams may provide more temporally benign environments (and potentially higher production) than others (Fig. 2b). Interestingly, these variables (baseflow stability and high flow variability) are not strongly correlated for these 20 streams ( $r = 0.37$ ), suggesting that many of these streams may have different hydrologic constraints.

#### *Land use will be a determinant of salmon production*

Land use activities at the watershed scale that enhance sediment input and thermal extremes of streams, such as large-scale clear cutting, row cropping, or construction, will have a negative effect on Atlantic salmon both indirectly by influencing prey production and directly by influencing fish mortality. For example, input of silt to a Minnesota stream from residential construction and agricultural activity in its upper watershed caused decreases in annual invertebrate production over a 5-year period (Waters 1982). Variation of brook trout (*Salvelinus fontinalis*) production followed an identical trend. This covariation was attributed either to food limitation of trout or to the negative effects of siltation on survivorship of both invertebrates and trout eggs and alevin (Waters 1982). Recent work in Michigan has demonstrated that the intensity of watershed-scale agricultural activity is much more important in explaining site-to-site variation in stream indices of local habitat and biotic integrity than is local riparian condition (Roth et al. 1996; Allan et al. 1997). Moderate amounts of agricultural land-use, however, have been shown to have a positive effect on Atlantic salmon production, presumably due to enhancement of the trophic basis for prey production in nutrient-poor watersheds (Kennedy et al. 1983; Bergheim and Hesthagen 1990; see also Johnston et al. 1990; Peterson et al. 1993).

**Fig. 3.** Hypothetical curves showing a linear (A) or threshold (B) response of juvenile salmon production to percentage of alluviated stream reaches at the watershed scale.



*Composite reach-structure will be a determinant of salmon production*

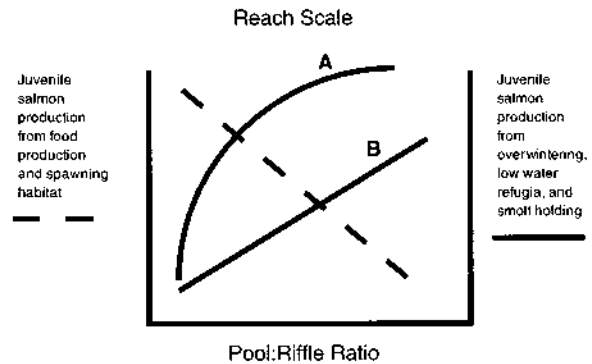
Factors likely to regulate total production potential for salmon at the watershed scale include the proportion of alluvial stream reaches, which provide both high quality food and non-foraging habitats. The degree to which salmon production may increase with alluviation, however, is not at all clear: production may increase relatively steadily with percent alluvial reaches (Fig. 3, line A), or it may remain relative flat until some threshold is passed (Fig. 3, line B). Clearly, the distinction would be important in terms of identifying suitable watersheds for Atlantic salmon restoration. Additionally, the spatial and temporal *connectivity* of stream reaches is critical to allow salmon to discover and exploit optimal habitat at the watershed scale. Selective barriers that restrict movement between reaches can greatly influence spatial patterns of salmon distribution and production. The effects of man-made barriers (e.g., dams) as barriers to efficient movement is well documented; however, the natural structures (e.g., waterfalls, beaver dams) at the local or reach scale can also exert a strong influence over watershed-level production (cf. Crowl et al. 1992; Schlosser 1995).

**Reach scale predictions**

*Proportion of trophic and non-trophic habitat will be a determinant of salmon production*

Maximum salmon production should occur under an optimal combination of trophic and non-trophic habitat types. For example, the relative availability of riffles and pools almost certainly influences salmon production. Bowlby and Roff (1986b) found that maximum biomass of multi-species salmonid assemblages sampled from 30 m long reaches in southern Ontario streams peaked at about 44% pool area. For Atlantic salmon, riffles are critical habitat for providing quality prey production and for spawning habitat, whereas pools serve important non-trophic functions, such as overwintering (Cunjak 1996), summer low flow refugia (Gibson 1988), or holding areas for smolts (R.A. Cunjak, Dept. Fish. and Oceans, personal communication). However, the frequency and (or) diversity of the various habitat types needed to maximize Atlantic salmon production is unknown (Gibson 1993; Cunjak 1996). Trophic habitat probably declines

**Fig. 4.** Hypothetical curves relating juvenile salmon production to stream the percentage of riffles and pools at the reach scale. Viewing the contribution of pools to production as non-linear (A) or linear (B) determines the optimum habitat configuration that supports maximum salmon production (points where the lines cross).



with increasing frequency of pools, but the degree to which the non-trophic function of pool habitat will contribute to potential salmon production is unknown. As an illustration, relatively few pools may be needed to ensure high survival of juveniles (Fig. 4, line A), or survival and subsequent production may increase relatively linearly with pool availability (Fig. 4, line B). In this hypothetical example, the fewer pools needed to ensure survival during bottleneck periods, the greater the potential salmon production in the reach. The slopes of these hypothetical curves might be expected to change as environmental conditions change, e.g., siltation (a watershed factor) would drive the food-production line down. Although this example is clearly an oversimplification of reality, it points to important potential tradeoff that needs some quantification if we are to understand geographic variation in limits to salmon production.

*Non-trophic habitat requirements may cause uncoupling of prey – salmon production relationships*

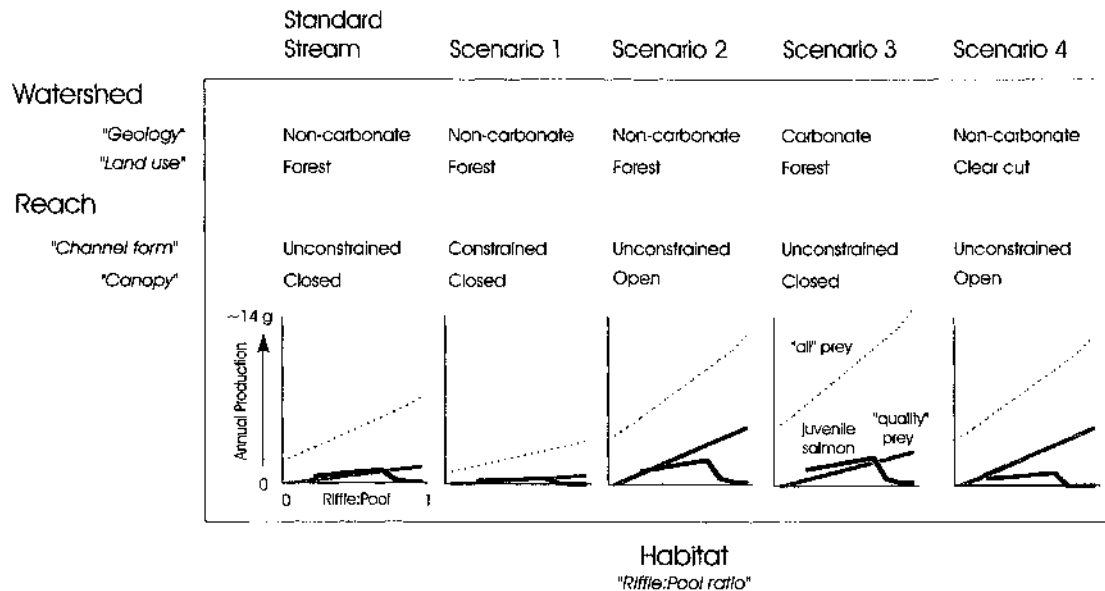
Depending on the interaction between non-trophic and trophic habitat requirements, the extent to which salmon are food-limited will vary with habitat structure. For example, in Fig. 4, the points of intersection of lines A and B indicate when limits on "carrying capacity" switch from food-limitation to non-food limitation. Until more is known about the interaction between non-trophic and trophic habitat requirements, the degree to which juvenile salmon production is coupled to invertebrate production will remain obscure.

**Local habitat-scale predictions**

*Availability of specific local-habitat types will control prey community composition and production*

Although this factor has received a great deal of study in temperate streams, there is little information about habitat-production relationships for prey communities in high latitude streams. The lack of this information renders recommendations about local-habitat types most favorable for salmon foraging speculative. Relative levels of prey production in pool versus riffle or bedrock outcrop in Atlantic salmon streams, for example, are for the most part unknown.

**Fig. 5.** A multi-scale view of selected factors suspected to influence secondary production in Atlantic salmon streams. The four quantitative scenarios presented in this figure are purely hypothetical, yet constrained to occur within realistic limits. These scenarios compare a hypothetical "standard stream" (left graph in all scenarios) to others that are influenced by factors operating at different levels within a spatial hierarchy (habitat, reach, watershed). See text for further explanation.



#### *Production of quality prey is a determinant of salmon production*

Prey – salmon production relationships based on measurements of gross prey production may obscure coupling between trophic levels, should these exist. Salmon production may be more profitably evaluated against the availability of high quality prey, both benthic (cf. Rader 1997) and terrestrial. Although processes operating at the reach scale will influence total prey quantity (e.g., proportion of trophic habitat available across the reach), the specific types of local habitat present will determine the production of quality prey for Atlantic salmon, because of the fundamental relationship between local habitat and invertebrate community composition.

#### **A synthesis**

An attempt to integrate selected physicochemical and non-trophic habitat limitations on invertebrate and salmon production in a multi-scale context is presented in Fig. 5. We provide these graphs as an heuristic device to show the value of conducting detailed production studies in a multi-scale framework and to highlight knowledge gaps about factors influencing production in salmon streams. Since comprehensive data do not exist, these quantitative scenarios are hypothetical, yet constrained to occur within realistic limits. The graphs predict how production of invertebrates and salmon respond to factors operating at three spatial scales: watershed, reach, and local habitat. An hypothetical "standard stream" of specified watershed and reach characteristics is used as a basis for comparing scale-dependent responses. Composite local habitat-scale effects are represented by a changing ratio of riffle to pool area; reach-scale effects are represented by contrasts in channel constraint and riparian-canopy cover; watershed-scale effects are represented by

contrasts in bedrock geology (non-carbonate versus carbonate) and land use (hardwood forest versus clearcut).

Our "standard stream" has an alluvial riffle-pool channel with a closed forest-canopy; riffles have coarse substrata and pools have fine sediments and are scoured during high flows; the watershed is forested and the bedrock is non-carbonate material. The composite local habitat ranges from 100% pool (extreme left of the X-axis on all graphs) to 100% riffle (extreme right). The Y-axis indicates hypothetical levels of habitat-weighted production expected for total benthic invertebrate prey, quality prey (sensu Rader 1997), and juvenile Atlantic salmon. Annual invertebrate production in riffles ( $7 \text{ g AFDM} \cdot \text{m}^{-2}$ ) and pools ( $2 \text{ g AFDM} \cdot \text{m}^{-2}$ ), and ratio of riffle to pool production (3.5) are based on reports for temperate streams with alluvial channels and mean discharge  $\sim 1 \text{ m}^3 \cdot \text{s}^{-1}$  (e.g., Benke 1993; Grubaugh et al. 1997). The proportion of production attributable to "quality prey" was set at 20% of riffle production, which is probably liberal for forested streams (cf. Huryn and Wallace 1987). Gross production efficiency of juvenile salmon was set at 20% for non-quality prey and 25% for quality prey. There is fairly good evidence to support the former efficiency (Waters 1988), but little evidence to support the latter, which may be conservative. Salmon were assumed capable of consuming all prey. Salmon production was assumed to be zero until pool habitat was reduced to less than 90% of the total stream area due to lack of sufficient riffle habitat for spawning. Once the pool habitat decreased to below 30% of the stream area, salmon production was reduced to reflect other non-trophic habitat limitation. There is no empirical basis for a precise threshold response as indicated on the graphs (cf. Fig. 4), so salmon production was simply decreased in proportion to the ratio of decreasing pool area to increasing riffle area. To examine how invertebrate and fish production respond to environmental factors at different hierarchical

scales, we manipulated reach-scale features (Scenarios 1 and 2) and watershed-scale features (Scenarios 3 and 4).

**Scenario 1.** The standard unconstrained alluvial reach is compared to a bedrock constrained reach in a forested, non-carbonate watershed. Annual macroinvertebrate production on the bedrock run habitat was set at  $3.5 \text{ g AFDM} \cdot \text{m}^{-2}$ , and production in pools was set at  $1 \text{ g AFDM} \cdot \text{m}^{-2}$ , or 50% of the production expected for alluvial riffle and pool habitats in similar size streams, a conservative difference assuming no moss cover (Purvis 1995). Salmon production was also reduced by 10% to reflect greater bioenergetic costs associated with foraging and maintaining position in this low-cover stream channel.

**Scenario 2.** The canopy has been removed from the standard stream, but the watershed remains forested beyond the channel margins. Production in riffles is increased  $1.7\times$  relative to the standard stream, following Behmer and Hawkins (1986), who showed a ratio of production in open riffles to shaded riffles ranging from 0.6 for filter-feeders to 2.8 for collector-gatherers and facultative grazers. Production in pools was increased  $2\times$  to reflect an overall increase in production because of enhanced quality of algal-derived detritus. The proportion of quality prey in the riffle habitat was doubled to 40% of total prey production, assuming a dramatic response of *Baetis* production after canopy removal (see Behmer and Hawkins 1986; Wallace and Gurtz 1986).

**Scenario 3.** The standard stream is modified to reflect a watershed-scale change in underlying geology of carbonate bedrock. Production in riffles and pools was increased  $2\times$ , which conservatively follows trends reported in the literature (Krueger and Waters 1983; Purvis 1995). However, although quality prey production also doubled, its proportion was not increased beyond the standard 20%, because significant amounts of production in carbonate streams are often in the form of armored organisms, such as snails (Huryn et al. 1995; Purvis 1995). We note, however, that amphipods can be abundant in some carbonate streams (e.g., Krueger and Waters 1983). In such cases, the proportion of quality prey as amphipod production might be more substantial in these streams.

**Scenario 4.** In this scenario, the standard non-carbonate watershed has been clearcut, which also causes opening of the canopy at the reach scale. Invertebrate production was increased in riffles ( $1.7\times$ ) and pools ( $2\times$ ) reflecting the positive effects of increased light, temperature, and nutrients. The proportion of quality prey was also increased to 40% of riffle production to reflect expected increases in baetids (see Scenario 2). Unlike Scenario 2, however, salmon production was reduced by 50% to reflect the negative effects of clear cutting on thermal regime and silt deposition on egg and alevin survival.

**Results.** In each scenario, maximum annual salmon production occurred when riffle area comprised 70% of total stream area. In the standard stream, peak salmon production was  $1.2 \text{ g AFDM} \cdot \text{m}^{-2}$ . Predictions of salmon production responded strongly to various scenarios of habitat alteration. Maximum annual salmon increased substantially when un-

derlying geology was changed at the watershed scale to carbonate bedrock ( $2.4 \text{ g AFDM} \cdot \text{m}^{-2}$  in Scenario 3) and when canopy conditions were opened at the reach scale ( $2.1 \text{ g AFDM} \cdot \text{m}^{-2}$  in Scenario 2). Minimum salmon production was predicted when reach-scale channel form was constrained bedrock ( $0.5 \text{ g AFDM} \cdot \text{m}^{-2}$  in Scenario 1). In Scenario 4, where both watershed-scale and reach-scale factors were modified, predicted annual salmon production was  $1.0 \text{ g AFDM} \cdot \text{m}^{-2}$ , a value similar to the standard stream. The range of predicted values falls within the range reported for Atlantic salmon streams, ca.  $0.2\text{--}1.6 \text{ g} \cdot \text{m}^{-2}$ , with  $3.1 \text{ g AFDM} \cdot \text{m}^{-2}$  being an extreme value from a carbonate watershed (Mann 1971). Certainly, the realism of these empirically based predictions about invertebrate and salmon production is questionable, given the gross assumptions and the extreme paucity of empirical data. Further, these predictions are based on short-term biotic responses to habitat alteration, and they do not take into account long-term geomorphic and ecological adjustments to habitat alteration. For example, while opening the canopy may stimulate short-term production of prey, removal of riparian trees can also result in a reduction of woody debris inputs to the stream channel. Subsequently, channel form may become simplified over time, resulting in reduced habitat complexity which can diminish cover for fish and may depress invertebrate production (see Gregory et al. 1991). Similarly, the prediction that clearcut watersheds with riparian canopy removal (Scenario 4) may produce as much salmon as the undisturbed standard stream does not take into account long-term habitat simplification, such as the reduction in pool frequency and size from siltation and loss of woody debris inputs (Bisson et al. 1992).

Despite these shortcomings, the scenarios are instructive because they allow us to visualize limitations to our knowledge about how multi-scale factors effect secondary production in streams. While the relationship between local habitat and production of stream invertebrates is firmly established, knowledge about how production might be influenced by factors operating at other spatial and temporal scales in the reach-watershed-region hierarchy are speculative. The scenarios do, however, allow us to posit several scale-dependent predictions that are relevant to both our earlier speculations (see "Predicting invertebrate and Atlantic salmon production at multiple scales," above) and to current and future research on Atlantic salmon (e.g., Armstrong et al. 1998; Parrish et al. 1998).

## Conclusions

Our ability to predict how multi-scale factors might influence the productivity of Atlantic salmon streams is clearly limited given the present state of stream ecology. This lack of knowledge about multi-scale factors is largely attributable to the traditionally selected unit of study: the local habitat. As a consequence, the relationship between invertebrate production and local habitat is fairly well understood for temperate latitude streams, while understanding of factors operating above the scale of the local habitat for streams at any latitude are based largely on speculation. Compared to the relatively detailed knowledge about invertebrate production, there seems to be little general understanding about

how trophic vs. non-trophic habitat influences salmon production at any scale. A predictive knowledge about salmon production across the geographic range of *Salmo salar* will require us to understand more clearly the dynamics of the relationship between trophic vs. non-trophic habitats and to define how this relationship changes with spatial scale — from local habitat on up the hierarchy.

## Acknowledgments

This paper was stimulated by a workshop held in Braemar, Scotland, in March 1997, entitled "Integrating across scales: predicting patterns of change in Atlantic salmon." We are very grateful for the support and vision of the Northeastern Forest Experimental Station of the USDA Forest Service (especially Richard Degraaf, Robert Lewis, and Keith Jensen). We also thank Joan Trial (Department of Inland Fisheries and Wildlife, Bangor, Maine) and David Halliwell for providing literature. NLP thanks Trout Unlimited for support during the development of this paper. Comments on an earlier draft by anonymous reviewers were also helpful in improving this paper.

## References

- Allan, J.D., Erickson, D.L., and Fay, J. 1997. The influence of catchment land use on stream integrity across multiple spatial scales. *Freshwater Biol.* **37**: 149–162.
- Allen, K.R. 1940. Studies on the biology of the early stages of the salmon (*Salmo salar*). 1. Growth in the River Eden. *J. Anim. Ecol.* **9**: 1–23.
- Angermeier, P.L. 1987. Spatiotemporal variation in habitat selection by fishes in Illinois streams. In *Community and evolutionary ecology of North American stream fishes*. Edited by W.J. Matthews and D.C. Heins. Univ. Oklahoma Press, Okla. pp. 52–60.
- 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.
- Bagenal, T. 1978. Methods for assessment of fish production in fresh waters. IBP Handbook No. 3. Blackwell Scientific Publications, Oxford.
- Ball, S.L., and Baker, R.L. 1996. Predator-induced life history changes: antipredator behavior costs or facultative life history shifts. *Ecology*, **77**: 1116–1124.
- Behmer, D.J., and Hawkins, C.P. 1986. Effects of overhead canopy on macroinvertebrate production in a Utah stream. *Freshwater Biol.* **16**: 287–300.
- Benke, A.C. 1984. Secondary production of aquatic insects. In *The ecology of aquatic insects*. Edited by V.H. Resh and D.M. Rosenberg. Praeger Publishers, New York. pp. 289–322.
- Benke, A.C. 1993. Concepts and patterns of invertebrate production in running waters. *Verh. Int. Verein. Limnol.* **25**: 15–38.
- Benke, A.C., Huryn, A.D., and Ward, G.M. 1997. Use of empirical models of stream invertebrate secondary production as applied to a functional feeding group. *Verh. Int. Verein. Limnol.* (In press.)
- Bergheim, A., and Hesthagen, T. 1990. Production of juvenile Atlantic salmon, *Salar salar* L., and brown trout, *Salmo trutta* L., within different sections of a small enriched Norwegian river. *J. Fish Biol.* **36**: 545–562.
- Bisson, P.A., Quinn, T.P., Reeves, G.H., and Gregory, S.V. 1992. Best management practices, cumulative effects, and long-term trends in fish abundance in Pacific Northwest river systems. In *Watershed management: balancing sustainability and environmental change*. Edited by R.J. Naiman. Springer-Verlag, New York, N.Y. pp. 189–223.
- Bowlby, J.H., and Roff, J.C. 1986a. Trophic structure in southern Ontario streams. *Ecology*, **67**: 1670–1679.
- Bowlby, J.H., and Roff, J.C. 1986b. Trout biomass and habitat relationships in southern Ontario streams. *Trans. Am. Fish. Soc.* **115**: 503–514.
- Cada, G.F., Loar, J.M., and Cox, D.K. 1987. Food and feeding preferences of rainbow and brown trout in southern Appalachian streams. *Am. Midl. Nat.* **117**: 374–385.
- Chapman, D.W. 1966a. Food and space as regulators of salmonid populations in streams. *Am. Nat.* **100**: 345–357.
- Chapman, D.W. 1966b. The relative contribution of aquatic and terrestrial primary producers to the trophic relations of stream organisms. Special publications of the Pymatuning Laboratory of Ecology, University of Pittsburgh, **4**: 116–130.
- Clifford, H.F. 1982. Life cycles of mayflies (Ephemeroptera), with special reference to voltinism. *Quaest. Entomol.* **18**: 15–90.
- Cloe, W.W., and Garman, G.C. 1996. The energetic importance of terrestrial arthropod inputs to three warm-water streams. *Freshwater Biol.* **36**: 105–114.
- Crowl, T.A., Townsend, C.R., and McIntosh, A.R. 1992. The impact of introduced brown and rainbow trout on native fish: the case of Australasia. *Rev. Fish Biol. Fish.* **2**: 217–241.
- Cummins, K.W. 1973. Trophic relations of aquatic insects. *Ann. Rev. Entomol.* **18**: 183–206.
- Cummins, K.W., Wilzbach, M.A., Gates, D.M., Perry, J.B., and Taliaferro, W.B. 1989. Shredders and riparian vegetation. *BioScience*, **39**: 24–30.
- Cunjak, R.A. 1988. Behaviour and microhabitat of young Atlantic salmon (*Salmo salar*) during winter. *Can. J. Fish. Aquat. Sci.* **53**(Suppl. 1): 267–282.
- Cunjak, R.A. 1996. Winter habitat of selected stream fishes and potential impacts from land-use activity. *Can. J. Fish. Aquat. Sci.* **53**(Suppl. 1): 267–282.
- Doucett, R.R., Power, G., Barton, D.R., Drimmie, R.J., and Cunjak, R.A. 1996. Stable isotope analysis of nutrient pathways leading to Atlantic Salmon. *Can. J. Fish. Aquat. Sci.* **53**: 2058–2066.
- Edwards, E.D., and Huryn, A.D. 1995. Annual contribution of terrestrial invertebrates to a New Zealand trout stream. *N.Z. J. Mar. Freshwater Res.* **29**: 465–475.
- Edwards, E.D., and Huryn, A.D. 1996. Effect of riparian land use on contributions of terrestrial invertebrates to streams. *Hydrobiologia*, **337**: 151–159.
- Egglishaw, H.J. 1967. The food, growth, and population structure of salmon and trout in two streams in the Scottish Highlands. *Freshwater Salmon Fish. Res.* **38**: 1–32.
- Egglishaw, H.J. 1970. Production of salmon and trout in a stream in Scotland. *J. Fish Biol.* **2**: 117–136.
- Egglishaw, H.J., and Shackley, P.E. 1977. Growth, survival and production of juvenile salmon and trout in a Scottish stream, 1966–75. *J. Fish Biol.* **11**: 647–672.
- Egglishaw, H.J., and Shackley, P.E. 1985. Factors governing the production of juvenile Atlantic salmon in Scottish streams. *J. Fish Biol.* **27**(Suppl. A): 27–33.
- Elliott, S.R., Coe, T.A., Helfield, J.M., and Naiman, R.J. 1998. Spatial variation in environmental characteristics of Atlantic salmon (*Salmo salar*) rivers. *Can. J. Fish. Aquat. Sci.* **55**(Suppl. 1): 267–280.

- Erkinaro, J., and Niemela, E. 1995. Growth differences between the Atlantic salmon parr, *Salmo salar*, of nursery brooks and natal rivers in the River Teno watercourse in northern Finland. *Environ. Biol. Fishes*, **42**: 277–287.
- Erman, D.C., Andrews, E.D., and Yoder-Williams, M. 1988. Effects of winter floods on fishes in the Sierra Nevada. *Can. J. Fish. Aquat. Sci.* **45**: 2195–2200.
- Fausch, K.D. 1998. Interspecific competition and juvenile Atlantic salmon (*Salmo salar*): on testing effects and evaluating the evidence across scales. *Can. J. Fish. Aquat. Sci.* **55**(Suppl. 1): 218–231.
- Fisher, S.G. 1977. Organic matter processing by a stream-segment ecosystem: Fort River, Massachusetts, U.S.A. *Int. Revue. Ges. Hydrobiol.* **62**: 701–727.
- Fisher, S.G., and Gray, L.J. 1983. Secondary production and organic matter processing by collector macroinvertebrates in a desert stream. *Ecology*, **64**: 1217–1224.
- Flecker, A.S., and Townsend, C.R. 1994. Community-wide consequences of trout introduction in New Zealand streams. *Ecol. Applic.* **4**: 798–807.
- Folt, C.L., Nislow, K.H., and Power, M.E. 1998. Implications of temporal and spatial scale for Atlantic salmon (*Salmo salar*) research. *Can. J. Fish. Aquat. Sci.* **55**(Suppl. 1): 9–21.
- Freeman, M.C., and Wallace, J.B. 1984. Production of net-spinning caddisflies (Hydropsychidae) and black flies (Simuliidae) on rock outcrop substrate in a small southeastern Piedmont stream. *Hydrobiologia*, **112**: 3–15.
- Frissell, C.A., and Nawa, R.K. 1992. Incidence and causes of physical failure of artificial fish habitat structures in streams of western Oregon and Washington. *N. Am. J. Fish. Manage.* **12**: 182–197.
- Frissell, C.A., Liss, W.J., Warren, C.E., and Hurley, M.D. 1986. A hierarchical framework for stream habitat classification: viewing streams in a watershed context. *Environ. Manage.* **10**: 199–214.
- Garman, G.C., and Moring, J.R. 1993. Diet and annual production of two boreal fishes following clearcut logging. *Environ. Biol. Fishes*, **36**: 301–311.
- Gee, A.S., Milner, N.J., and Hemsworth, R.J. 1978. The production of juvenile Atlantic salmon, *Salmo salar* in the upper Wye, Wales. *J. Fish Biol.* **13**: 439–451.
- Gibson, R.J. 1978. The behaviour of juvenile Atlantic salmon (*Salmo salar*) and brook trout (*Salvelinus fontinalis*) with regard to temperature and to water velocity. *Trans. Am. Fish. Soc.* **107**: 703–712.
- Gibson, R.J. 1988. Mechanisms regulating species composition, population structure and production of stream salmonids: a review. *Pol. Arch. Hydrobiol.* **35**: 469–495.
- 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 Cunjak, R.A. 1986. An investigation of competitive interactions between brown trout (*Salmo trutta* L.) and juvenile Atlantic salmon (*Salmo salar* L.) in rivers of the Avalon Peninsula, Newfoundland. *Can. Tech. Rep. Fish. Aquat. Sci.* No. 1472.
- Gibson, R.J., and Dickson, T.A. 1984. The effects of competition on the growth of juvenile Atlantic salmon. *Nat. Can. (Que.)*, **111**: 175–191.
- Gibson, R.J., and Galbraith, D. 1975. The relationships between invertebrate drift and salmonid populations in the Matamek River, Quebec, below a lake. *Trans. Am. Fish. Soc.* **104**: 529–535.
- Gibson, R.J., Stansbury, D.E., Whalen, R.R., and Hillier, K.G. 1993. Relative habitat use, and inter-specific and intra-specific competition of brook trout (*Salvelinus fontinalis*) and juvenile Atlantic salmon (*Salmo salar*) in some Newfoundland rivers. In *Production of juvenile Atlantic salmon, Salmo salar, in natural waters. Edited by R.J. Gibson and R.E. Cutting. Can. Spec. Publ. Fish. Aquat. Sci.* **118**. pp. 53–96.
- Gotceitas, V., and Godin, J.-G. 1993. Effects of aerial and in-stream threat of predation on foraging by Atlantic salmon (*Salmo salar*). In *Production of juvenile Atlantic salmon, Salmo salar, in natural waters. Edited by R.J. Gibson and R.E. Cutting. Can. Spec. Publ. Fish. Aquat. Sci.* **118**. pp. 35–41.
- Gregory, S.V., Swanson, F.J., and McKee, W.A. 1991. An ecosystem perspective of riparian zones. *BioScience*, **41**: 540–551.
- Gresens, S.E. 1997. Interactive effects of diet and thermal regime on growth of the midge *Pseudochironomus richardsoni* Malloch. *Freshwater Biol.* **38**: 365–373.
- Grubaugh, J.W., and Wallace, J.B. 1995. Functional structure and production of the benthic community in a Piedmont river: 1956–1957 and 1991–1992. *Limnol. Oceanogr.* **40**: 490–501.
- Grubaugh, J.W., Wallace, J.B., and Houston, E.S. 1997. Production of benthic macroinvertebrate communities along a southern Appalachian river continuum. *Freshwater Biol.* **37**: 581–596.
- Harvey, B.C. 1987. Susceptibility of young-of-the-year fishes to downstream displacement by flooding. *Trans. Am. Fish. Soc.* **116**: 851–855.
- Havey, K.A., and Davis, R.M. 1970. Factors influencing standing crops and survival of juvenile salmon at Barrows Stream, Maine. *Trans. Am. Fish. Soc.* **99**: 297–311.
- Hawkins, C.P., Kershner, J.L., Bisson, P.A., Bryant, M.D., Decker, L.M., Gregory, S.V., McCullough, D.A., Overton, C.K., Reeves, G.H., Steedman, R.J., and Young, M.K. 1993. A hierarchical approach to classifying stream habitat features. *Fisheries*, **18**(6): 3–10.
- Hegggenes, J., and R. Borgstrom. 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.
- Hill, W.R. 1992. Food limitation and interspecific competition in snail-dominated streams. *Can. J. Fish. Aquat. Sci.* **49**: 1257–1267.
- Hudon, C. 1994. Biological events during ice breakup in the Great Whale River (Hudson Bay). *Can. J. Fish. Aquat. Sci.* **51**: 2467–2481.
- Hunt, R.L. 1975. Food relations and behaviour of salmonid fishes. In *Coupling of land and water systems. Edited by A.D. Hasler. Springer Verlag, New York, N.Y.* pp. 137–151.
- Hurn, A.D. 1996. An appraisal of the Allen paradox in a New Zealand trout stream. *Limnol. Oceanogr.* **41**: 243–252.
- Hurn, A.D. 1998. Ecosystem-level evidence for top-down and bottom-up control of production in a grassland stream system. *Oecologia*, **115**: 173–183.
- Hurn, A.D., and Wallace, J.B. 1987. Local geomorphology as a determinant of macrofaunal production in a mountain stream. *Ecology*, **68**: 1932–1942.
- Hurn, A.D., Benke, A.C., and Ward, G.M. 1995. Direct and indirect effects of regional geology on the distribution, production and biomass of the freshwater snail *Elimia*. *J. N. Am. Benthol. Soc.* **14**: 519–534.
- Hynes, H.B.N. 1970. *The ecology of running waters.* University of Toronto Press, Toronto, Ont.
- Imhof, J. G., Fitzgibbon, J., and Annable, W. K. 1996. A hierarchical evaluation system for characterizing watershed ecosystems for fish habitat. *Can. J. Fish. Aquat. Sci.* **53**(Suppl. 1): 312–326.
- Jacobi, D.I., and Benke, A.C. 1991. Life histories and abundance patterns of snag-dwelling mayflies in a blackwater Coastal Plain river. *J. N. Am. Benthol. Soc.* **10**: 372–387.



- Jensen, A.J., and Johnsen, B.O. 1986. Different adaptation strategies of Atlantic salmon (*Salmo salar*) populations to extreme climates with special reference to some cold Norwegian rivers. *Can. J. Fish. Aquat. Sci.* **43**: 980-984.
- Johnston, N.T., Perrin, C.J., Slaney, P.A., and Ward, B.R. 1990. Increased juvenile salmonid growth by whole-river fertilization. *Can. J. Fish. Aquat. Sci.* **47**: 862-872.
- Kennedy, G.J.A., Cragg-Hinc, D., and strange, C.D. 1983. The effect of a land scheme on the salmonid population of the River Camowen, Co. Tyrone. *Fish Manage.* **14**: 1-6.
- Krueger, C.C., and Waters, T.F. 1983. Annual production of macroinvertebrates in three streams of different water quality. *Ecology*, **64**: 840-850.
- Kwak, T.J., and Waters, T.F. 1997. Trout production dynamics and water quality in Minnesota streams. *Trans. Am. Fish. Soc.* **126**: 35-48.
- Lancaster, J., and A. Hildrew. 1993. Characterizing in-stream flow refugia. *Can. J. Fish. Aquat. Sci.* **50**: 1663-1675.
- Lindroth, A. 1965. The Baltic salmon stock. Its natural and artificial regulation. *Mitt. Int. Verein. Limnol.* **13**: 163-192.
- Mann, R.H.K. 1971. The populations, growth, and production of fish in four small streams in southern England. *J. Anim. Ecol.* **40**: 155-190.
- Mason, C.F., and Macdonald, S.M. 1982. The input of terrestrial invertebrates from tree canopies to a stream. *Freshwater Biol.* **12**: 305-311.
- Mason, J.C. 1976. Response of underyearling coho salmon to supplemental feeding in a natural stream. *J. Wildlife Manage.* **40**: 775-788.
- McIntosh, A.R., and Townsend, C.R. 1995. Impacts of an introduced predatory fish on mayfly grazing in New Zealand streams. *Limnol. Oceanogr.* **40**: 1508-1512.
- McIntosh, A.R., and Townsend C.R. 1996. Interactions between fish, grazing invertebrates and algae in a New Zealand stream: a trophic cascade mediated by fish-induced changes to grazer behaviour? *Oecologia*, **108**: 174-181.
- McPeck, M.A., and Peckarsky, B.L. 1998. Life histories and the strength of species interactions: combining mortality, growth, and fecundity effects. *Ecology*, **79**: 867-879.
- Mcisner, J.D., Rosenfeld, J.S., and Regier, H.A. 1988. The role of groundwater in the impact of climate warming on stream salmonines. *Fisheries*, **13**: 2-8.
- Meister, A.L. 1962. Atlantic salmon production in Cove Brook, Maine. *Trans. Am. Fish. Soc.* **91**: 208-212.
- Metcalf, N.B., Huntingford, F., and Thorpe, J.E. 1987. The influence of predation risk on the feeding motivation and foraging strategy of juvenile Atlantic salmon. *Anim. Behav.* **35**: 901-911.
- Mills, D. 1989. *Ecology and management of Atlantic salmon*. Chapman and Hall, London.
- Montgomery, D.R., Abbe, T.B., Buffington, J.M., Peterson, N.P., Schmidt, K.M., and Stock, J.D. 1996. Distribution of bedrock and alluvial channels in forested mountain drainages. *Nature*, **381**: 587-589.
- Moore, K.M.S., and Gregory, S.V. 1988. Response of young-of-the-year cutthroat trout to manipulation of habitat structure in a small stream. *Trans. Am. Fish. Soc.* **117**: 162-170.
- Morin, A., and Bourassa, N. 1992. Modeles empiriques de la production annuelle de du rapport P/B d'invertebrates benthiques d'eau courante. *Can. J. Fish. Aquat. Sci.* **49**: 532-539.
- Morin, A., and Dumont, P. 1994. A simple model to estimate growth rate of lotic insect larvae and its value for estimating population and community production. *J. N. Am. Benthol. Soc.* **13**: 357-367.
- Murphy, M.L., Hawkins, C.P., and Anderson, N.H. 1981. Effects of canopy modifications and accumulated sediment on stream communities. *Trans. Am. Fish. Soc.* **110**: 469-178.
- Nelson, J.M. 1965. A seasonal study of aerial insects close to a moorland stream. *J. Anim. Ecol.* **34**: 573-579.
- Neves, R. J. 1979. Secondary production of epilithic fauna in a woodland stream. *Am. Midl. Nat.* **102**: 209-224.
- Nislow, K.H., Folt, C.L., and Seandel, M. 1998. Food and foraging behavior in relation to microhabitat use and survival of age-0 Atlantic salmon. *Can. J. Fish. Aquat. Sci.* **55**: 116-127.
- O'Hop, J., Wallace, J.B., and Haefner, J.D. 1985. Production of a stream shredder, *Peltoperla maria* (Plecoptera: Peltoperlidae) in disturbed and undisturbed hardwood catchments. *Freshwater Biol.* **14**: 13-21.
- Palmer, M.A., Arensburger, P., Martin, A.P., and Denman, D.W. 1996. Disturbance and patch-specific responses: the interactive effects of woody debris and floods on lotic invertebrates. *Oecologia*, **105**: 247-257.
- Parrish, D.L., Behnke, R.J., Gephard, S.R., McCormick, S.D., and Reeves, G.H. 1998. Why aren't there more Atlantic salmon (*Salmo salar*)? *Can. J. Fish. Aquat. Sci.* **55**(Suppl. 1): 281-287.
- Pearsons, T.N., Li, H.W., and Lamberti, G.A. 1992. Influence of habitat complexity on resistance to flooding and resilience of stream fish assemblages. *Trans. Am. Fish. Soc.* **121**: 427-436.
- Peckarsky, B.L., and McIntosh, A.R. 1998. Fitness and community consequences of avoiding multiple predators. *Oecologia*, **113**: 565-576.
- Peterson, B.J., and 16 others. 1993. Biological responses of a tundra river to fertilization. *Ecology*, **74**: 653-672.
- Poff, N.L. 1996. A hydrogeography of unregulated streams in the United States and an examination of scale-dependence in some hydrological descriptors. *Freshwater Biol.* **36**: 71-91.
- Poff, N.L. 1997. Landscape filters and species traits: towards mechanistic understanding and prediction in stream ecology. *J. N. Am. Benthol. Soc.* **16**: 391-409.
- Poff, N.L., and Ward, J.V. 1989. Implications of streamflow variability and predictability for lotic community structure: a regional analysis of streamflow patterns. *Can. J. Fish. Aquat. Sci.* **46**: 1805-1818.
- Poff, N.L., and J.V. Ward. 1990. The physical habitat template of lotic systems: recovery in the context of historical pattern of spatio-temporal heterogeneity. *Environ. Manage.* **14**: 629-646.
- Poff, N.L., Allan, J.D., Bain, M.B., Karr, J.R., Prestegard, K.L., Richter, B., Sparks, R., and Stromberg, J. 1997. The natural flow regime: a new paradigm for riverine conservation and restoration. *BioScience*, **47**: 769-784.
- Power, M., and Power, G. 1992. Modeling the dynamics of smolt production in Atlantic salmon. *Trans. Am. Fish. Soc.* **123**: 535-548.
- Power, M.E. 1992. Hydrologic and trophic controls of seasonal algal blooms in northern California rivers. *Arch. Hydrobiol.* **125**: 385-410.
- Power, M.E., Parker, M.S., and Wootton, J.T. 1996. Disturbance and food chain length in rivers. *In Food webs: integration of patterns and dynamics*. Edited by G.A. Polis and K.O. Winemiller. Chapman and Hall, New York, N.Y. pp. 286-297.
- Purvis, J.M. 1995. Effects of geology on watershed geomorphology and the ecology of grazing stream invertebrates. Ph.D. dissertation. University of Alabama, Tuscaloosa, Ala.
- Rabeni, C.F., and Sowa, S.P. 1996. Integrating biological realism into habitat restoration and conservation strategies for small streams. *Can. J. Fish. Aquat. Sci.* **53**(Suppl. 1): 252-259.

- Rader, R.B. 1997. A functional classification of the drift: traits that influence invertebrate availability to salmonids. *Can. J. Fish. Aquat. Sci.* **54**: 1–24.
- Randall, R.G., and Chadwick, E.M.P. 1986. Density as a factor affecting the production of juvenile Atlantic salmon (*Salmo salar*) in the Miramichi and Restigouche Rivers, New Brunswick. *Pol. Arch. Hydrobiol.* **33**: 391–407.
- Randall, R.G., and Paim, U. 1982. Growth, biomass, and production of juvenile Atlantic salmon (*Salmo salar* L.) in two Miramichi River, New Brunswick, tributary streams. *Can. J. Zool.* **60**: 1647–1659.
- Randall, R.G., Kelso, J.R.M., and Minns, C.K. 1995. Fish production in freshwaters: are rivers more productive than lakes? *Can. J. Fish. Aquat. Sci.* **52**: 631–643.
- Resh, V.H., and Rosenberg, D.M. 1984. *The ecology of aquatic insects*. Praeger, New York.
- Resh, V.H., Brown, A.V., Covich, A.P., Gurtz, M.E., Li, H.W., Minshall, G.W., Reice, S.R., Sheldon, A.L., Wallace, J.B., and Wissmar, R. 1988. The role of disturbance in stream ecology. *J. N. Am. Benthol. Soc.* **7**: 433–455.
- Richards, C., Johnson, L.B., and Host, G.E. 1996. Landscape-scale influences on stream habitats and biota. *Can. J. Fish. Aquat. Sci.* **53**(Suppl. 1): 295–311.
- Richardson, J.S. 1991. Seasonal food limitation of detritivores in a montane stream: an experimental test. *Ecology*, **72**: 873–887.
- Richardson, J.S. 1993. Limits to productivity in streams: evidence from studies of macroinvertebrates. *In* Production of juvenile Atlantic salmon, *Salmo salar*, in natural waters. *Edited by* R.J. Gibson and R.E. Cutting. *Can. Spec. Publ. Fish. Aquat. Sci.* **118**. pp. 9–15.
- Ross, H.H. 1963. Stream communities and terrestrial biomes. *Arch. Hydrobiol.* **59**: 235–242.
- Roth, N.E., Allan, J.D., and Erickson, D.L. 1996. Landscape influences on stream biotic integrity assessed at multiple spatial scales. *Landscape Ecol.* **11**: 141–156.
- Sallenne, R.M., and Day, K.E. 1991. Secondary production of benthic stream invertebrates in agricultural watersheds with different land management practices. *Chemosphere*, **23**: 57–76.
- Sanchez, M.R., and Hendricks, A.C. 1997. Life history and secondary production of Cheumatopsyche spp. in a small Appalachian stream with two different land uses on its watershed. *Hydrobiologia*, **354**: 127–139.
- Scarsbrook, M.R., and Townsend, C.R. 1993. Stream community structure in relation to spatial and temporal variation: a habitat templet study of two contrasting New Zealand stream. *Freshwater Biol.* **29**: 395–410.
- Schlösser, I.J. 1991. Stream fish ecology: a landscape perspective. *BioScience*, **41**: 704–712.
- Schlösser, I.J. 1995. Dispersal, boundary processes, and trophic-level interactions in streams adjacent to beaver ponds. *Ecology*, **76**: 908–925.
- Slaney, P.A., and Northcote, T.G. 1974. Effects of prey abundance on density and territorial behavior of young rainbow trout (*Salmo gairdneri*) in laboratory stream channels. *J. Fish. Res. Board Can.* **31**: 1201–1209.
- Sweeney, B.W. 1984. Factors influencing life-history patterns of aquatic insects. *In* The ecology of aquatic insects. *Edited by* V.H. Resh and D.M. Rosenberg. Praeger Publishers, New York, N.Y. pp. 56–100.
- Townsend, C.R., and Hildrew, A.G. 1994. Species traits in relation to a habitat templet for river systems. *Freshwater Biol.* **31**: 265–276.
- Vannote, R.L., Minshall, G.W., Cummins, K.W., Sedell, J.R., and Cushing, C.E. 1980. The river continuum concept. *Can. J. Fish. Aquat. Sci.* **37**: 130–137.
- Wallace, J.B., and Gurtz, M.E. 1986. Responses of *Baetis* mayflies (Ephemeroptera) to catchment logging. *Am. Midl. Nat.* **115**: 25–41.
- Waters, T.F. 1969. The turnover ratio in production ecology of freshwater invertebrates. *Am. Nat.* **103**: 173–185.
- Waters, T.F. 1972. The drift of stream insects. *Annu. Rev. Entomol.* **17**: 253–272.
- Waters, T.F. 1982. Annual production by a stream brook charr population and its principal invertebrate food. *Environ. Biol. Fish.* **7**: 165–170.
- Waters, T.F. 1988. Fish production – benthos production relationships in trout streams. *Pol. Arch. Hydrobiol.* **35**: 545–561.
- Waters, T.F. 1992. Annual production, production/biomass ratio, and the ecotrophic coefficient for management of trout in streams. *N. Am. J. Fish. Manage.* **12**: 34–39.
- Waters, T.F. 1993. Dynamics in stream ecology. *In* Production of juvenile Atlantic salmon, *Salmo salar*, in natural waters. *Edited by* R.J. Gibson and R.E. Cutting. *Can. Spec. Publ. Fish. Aquat. Sci.* **118**. pp. 1–8.
- Webster, J.R., Wallace, J.B., and Benfield, E.F. 1995. Organic processes in streams of the eastern United States. *In* Ecosystems of the world 22: river and stream ecosystems. *Edited by* C.E. Cushing, K.W. Cummins, and G.W. Minshall. Elsevier, Amsterdam. pp. 117–187.
- Wiggins, G.B., and Mackay, R.J. 1978. Some relationships between systematics and trophic ecology in Nearctic aquatic insects with special reference to Trichoptera. *Ecology*, **59**: 1211–1220.
- Wilzbach, M.A., Cummins, K.W., and Hall, J.D. 1986. Influence of habitat manipulations on interactions between cutthroat trout and invertebrate drift. *Ecology*, **67**: 898–911.
- Wipfli, M.S. 1997. Terrestrial invertebrates as salmonid prey and nitrogen sources in streams: contrasting old-growth and young-growth riparian forests in southeastern Alaska, USA. *Can. J. Fish. Aquat. Sci.* **54**: 1259–1269.
- Wootton, J.T., Parker, M.S., and Power, M.E. 1996. Effects of disturbance on river food webs. *Science* **273**: 1558–1561.