

A new method to identify the fluvial regimes used by spawning salmonids

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Abstract: Basin physiography and fluvial processes structure the availability of salmonid spawning habitat in river networks. However, methods that allow us to explicitly link hydrologic and geomorphic processes to spatial patterns of spawning at scales relevant to management are limited. Here we present a method that can be used to link the abundance of spawning salmonids to fluvial processes at the mesoscale. We show that the frequency of spawning activity at individual morphological units (riffles, pools, runs) is quantitatively related to a number of fluvial parameters. Of these, bankfull excess shear stress (τ_{xs}) was the best predictor of spawning frequency. Results suggest that τ_{xs} can be used to represent the fluvial regimes that spawning salmon are responsive to as well as to assess the likely impacts of altered flow regimes.

Résumé : La physiographie du bassin et les processus fluviaux sont responsables de la disponibilité de l'habitat de fraie des salmonidés dans les réseaux de rivières. Il y a cependant peu de méthodes qui permettent de relier explicitement les processus hydrologiques et géomorphiques aux patrons spatiaux de la fraie à des échelles qui sont pertinentes à la gestion. Nous présentons ici une méthode qui peut servir à relier l'abondance de salmonidés en fraie aux processus fluviaux à une échelle moyenne. Nous démontrons que la fréquence de l'activité de fraie dans des unités morphologiques particulières (les rapides, fosses et coulées) est associée quantitativement à un certain nombre de variables fluviales. Parmi celles-ci, la contrainte de cisaillement en excès à pleins bords (τ_{xs}) est la meilleure variable prédictive de la fréquence de fraie. Nos résultats indiquent que τ_{xs} peut servir à représenter les régimes fluviaux auxquels les saumons réagissent, ainsi qu'à évaluer les impacts probables des modifications des régimes d'écoulement.

[Traduit par la Rédaction]

Introduction

Sustainable river management is only possible if we understand the links between species, the habitats they use, and the physical processes creating these habitats. This understanding is needed most for life stages that exert an important influence on species' reproductive success. Moreover, our understanding needs to be at scales relevant to management, whether it be the development of environmental flow regimes in regulated systems or habitat restoration in physically degraded channels.

Spawning is a critical stage in the life cycle of salmonid fish (Quinn 2005). Salmonids generally spawn in gravel- and cobble-bed rivers, preferentially within pool-riffle channels (Montgomery et al. 1999). The hydraulic and sedimentary characteristics of the specific locations used by

spawning fish are well documented (e.g., Moir et al. 2002) but this microscale analysis is data intensive and hence costly. Conversely, reach-scale analysis does not capture the subreach conditions that fish are selecting when spawning. An intermediate, mesoscale analysis applied to individual morphologic units (e.g., riffles, bars, runs) may be most appropriate for determining meaningful relationships between physical conditions and spawning (Fig. 1). We used this scale of analysis to investigate fluvial controls on spawning activity of Atlantic salmon (*Salmo salar*) in an upland Scottish stream. We do not aim to understand why salmon use some areas and not others; the broad geomorphic controls on spawning and nonspawning locations within river systems and the microhabitat conditions selected and avoided by fish are already known and detailed in the literature (e.g., Montgomery et al. 1999; Moir et al. 2004). Rather,

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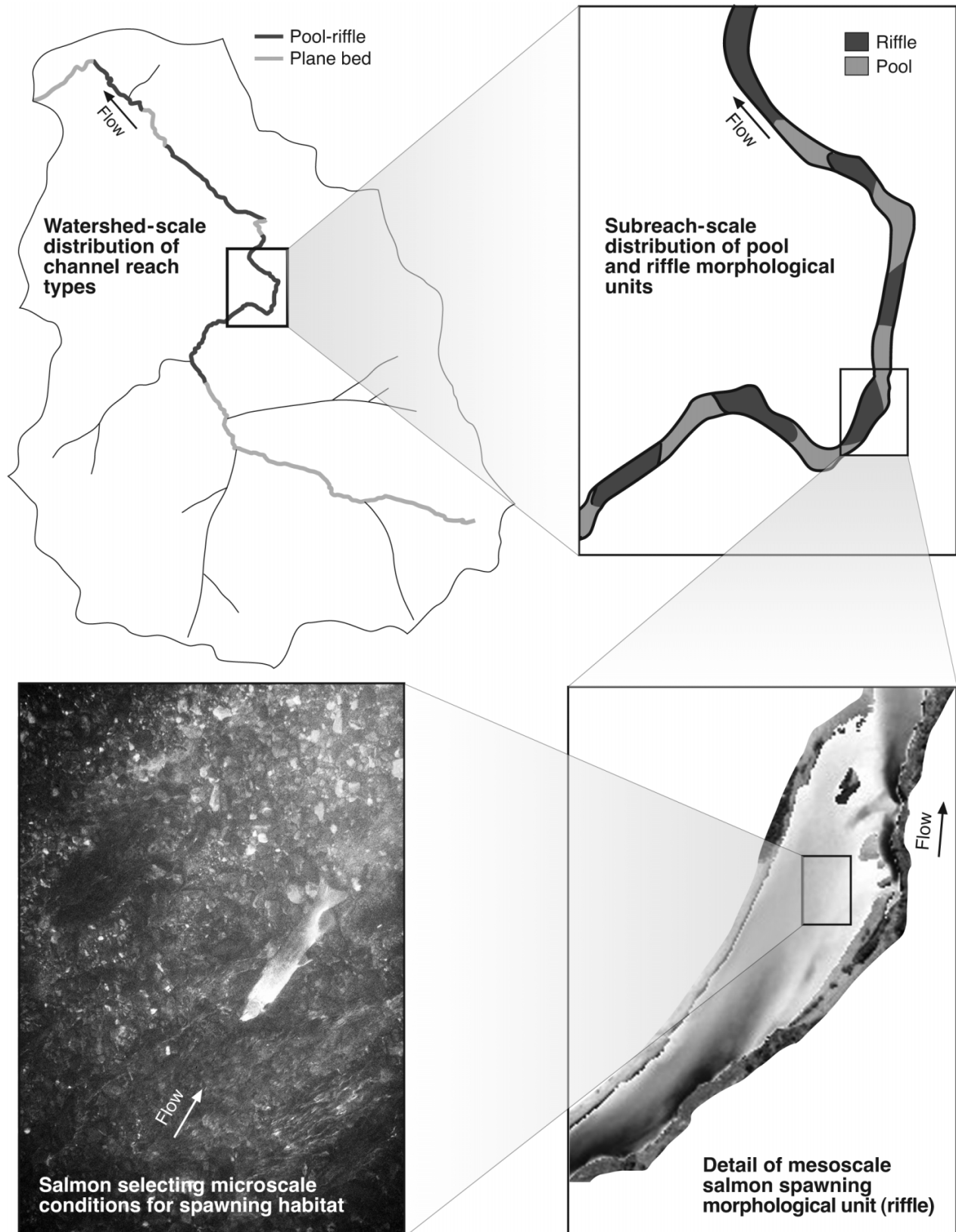
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Fig. 1. Conceptual diagram of the nested hierarchy of spatial scales present in river systems that influence the spatial distribution of salmonid spawning habitat. Spatial scales decrease from the top left corner in a clockwise direction. Our study focuses on mesoscale morphological units (e.g., riffle, run).



we aim to relate observed mesoscale variation of spawning activity to fluvial characteristics that create spawning habitat.

Materials and methods

Study area and spawning observations

The Allt a' Ghlinne Bhig (56°49'N, 3°27'W) is a small (27 km²), unregulated mountain tributary of the River Tay. Spawning observations were made in the stream in five years (2000–2003, 2006, and 2007). In each year, surveys began on the day of commencement of spawning activity and continued until only sporadic incidents were detected (Moir et al. 2006). On each day, the same experienced observer walked the stream from the mouth (335 m above mean sea level) to the upstream limit of spawning (a waterfall impassable to fish 9.1 km upstream at 510 m above mean sea level) in daylight hours (08:00 to 16:00); on average, surveys were conducted on 86% of the days over the studied spawning periods. Spawning (initial cutting and oviposition) was defined using recognized criteria (Jones 1959). The location of spawning incidents was determined using a hand-held Global Positioning System.

Study locations

Spawning sites in upland streams occur over a continuum of spatial scales from entire morphological units to small (<3 m²) localized gravel accumulations (Moir et al. 2004). Spawning incidents in the gravel accumulations do not reflect morphological unit scale processes but, rather, much smaller scale factors (e.g., localized deposition of gravels behind large boulders) that result in transient areas of suitable habitat. For this analysis, we used only locations that supported, on average, one or more spawning incidents per year per unit channel length over the course of the study (i.e., greater than five spawning incidents in total). This criterion provided a clear division between clusters of spawning activity associated with specific morphological units (the focus of this study) and more sporadic incidents in small gravel accumulations.

A total station was used to conduct topographical surveys of potential sites in September and October 2003. The surveys determined mean bank-full width, depth, and longitudinal bed slope (the latter measured between geomorphically equivalent topographic highs, e.g., riffle/bar crests or boulder steps). Once the subsample of these sites that met the greater than five spawning incident criterion was determined, an assessment was made from photographic time series as to whether significant morphological change had occurred between 2000 and 2007; sites where such change had occurred (either before or after the 2003 survey) were removed. The same observer walked the entire stream on each day in each year and became sufficiently familiar with the characteristics of the channel to identify significant morphological change. Although small variations in the structure and sedimentology of bedforms occurred, the mesoscale focus of study sites meant that marked change to general channel geometry (e.g., bank-full width and depth and bed slope) would be required for exclusion of sites from the study. The 37 sites that were identified by this two-stage procedure accounted for 552 of the 726 (76%) observed

spawning incidents. The sites extended across an 8.2 km length of the stream (from the mouth to within 0.9 km of the farthest upstream point accessible to adult salmon).

Characterization of fluvial regime

Our analysis focused on fluvial characteristics that create spawning habitat. As such, five channel-forming parameters were examined: total stream power (Ω), specific stream power (ω), shear stress (τ), excess specific stream power (ω_{xs}), and excess shear stress (τ_{xs}), with the latter two describing the degree of bed mobility at a given flow. All parameters were calculated using standard equations available in the literature and are further defined in the list of symbols. The parameters were evaluated for bank-full flow, since the hydraulic conditions at this flow exert a dominant control on channel morphology in many alluvial rivers (Wolman and Miller 1960), i.e., bank-full is a geomorphically significant flow. So that ω_{xs} and τ_{xs} were relevant to salmon spawning habitat, we expressed these parameters as the difference between bank-full conditions and critical values for mobilizing the median size of sediment used by spawning fish ($D_{50} = 41.1$ mm, determined from nearby spawning tributaries; Moir et al. 2002). It is important to note that the above parameters do not describe the micro-scale physical conditions at the time of spawning but rather describe the mesoscale fluvial regime of spawning habitats during channel-forming flows.

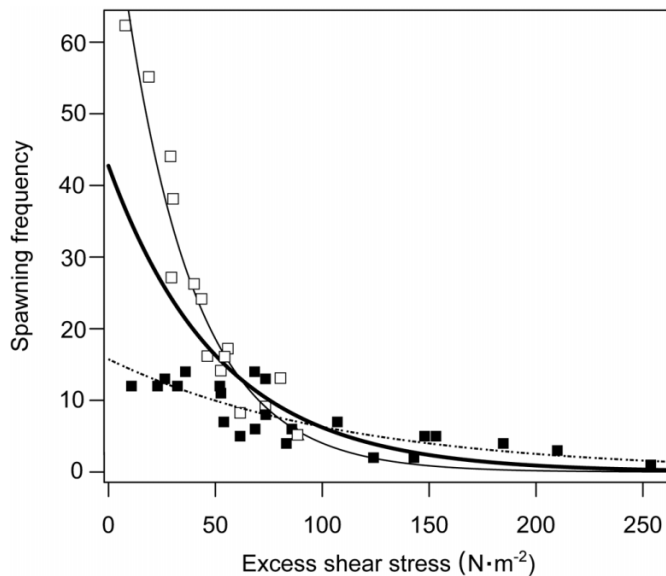
Results

Parameter τ_{xs} was the best predictor of spawning frequency (Ω , $R^2 = 0.11$; ω , $R^2 = 0.45$; τ , $R^2 = 0.53$; ω_{xs} , $R^2 = 0.57$; τ_{xs} , $R^2 = 0.67$; all $n = 37$). However, there was still an appreciable amount of the variation that remained unexplained by this parameter alone, particularly at $\tau_{xs} < 50$ N·m⁻² (Fig. 2). The data set was therefore subdivided to show separate relationships for river sections upstream and downstream of a major tributary confluence within the study basin (the rationale for separating the stream at this point was that the confluence marked an abrupt change in drainage area and, hence, channel discharge and dimensions). Separate curves fitted to each of the two sections (downstream: $R^2 = 0.90$, $P < 0.001$, $n = 15$; upstream: $R^2 = 0.71$, $P < 0.001$, $n = 23$) showed a significantly improved fit over the single regression ($R^2 = 0.67$). Many more fish used locations with $\tau_{xs} < 50$ N·m⁻² in the downstream river section compared with the upstream one.

Discussion

Our analysis demonstrates that the frequency of spawning by Atlantic salmon is inversely related to τ_{xs} . Given the explicit mesoscale of our analysis and the fact that τ_{xs} was indexed to a single discharge (bank-full flow), this relationship should not be interpreted as meaning that fish construct redds at points that have particular values of τ_{xs} at the time of spawning. Rather, the results indicate that spawning occurs most frequently in morphological units that, at a geomorphically effective flow, have low mobility of spawning sediment. Low sediment mobility has several possible consequences for salmon habitat. It may influence the availability of spawning gravels, particularly for bank-full threshold

Fig. 2. Regressions between spawning frequency and excess shear stress. Open squares, downstream river section; solid squares, upstream river section; thick curve, overall regression for entire data set; broken curve, regression for upstream section; thin curve, regression for downstream section.



channels, where the size of material on the bed will approach the spawning sediment size as τ_{xs} approaches zero (Buffington and Montgomery 1999), assuming no sediment supply limitations. Alternatively, τ_{xs} is directly related to probability of scour (Haschenburger 1999), with potentially greater productivity and higher numbers of fish returning to sites that are less likely to scour incubating eggs. The τ_{xs} can also be an index of channel morphology (García et al. 2000) and associated depth and velocity regimes (Moir et al. 2006). Our analysis does not allow examination of these factors, so further investigation of the biological significance of low τ_{xs} values is warranted.

At lower τ_{xs} values, the number of fish using particular locations differed markedly between the two sections of the stream. This divergence, as well as the improved fit of the relationship when subdivided by river section, indicates that there are location-specific factors that influence the interaction between fish and physical habitat conditions. Our data do not allow us to isolate the cause of the different relationships in the two sections, but there are a number of possible explanations. The larger drainage area of the downstream section will produce relatively larger channel dimensions with potentially more spawning area per mesoscale unit and thus a greater carrying capacity. However, in this study, a similar number of locations with $\tau_{xs} < 50 \text{ N}\cdot\text{m}^{-2}$ were present in both the downstream and upstream sections, and differences in area between channel units in the two sections were not sufficient to explain variations in spawning frequency. The explanation therefore may be a biological one. For example, differences in juvenile production and their fine-scale homing behaviour when they return as adults (Youngson et al. 1994) may lead to different patterns of occupancy along the stream. There may also be differences in competition and predation between the stream sections that contribute to differences in frequency of use.

Overall, the results indicate that there are clear relationships between τ_{xs} and spawning frequency, and the strength of these improve when spawning locations are grouped according to position within the stream network. Indexing the fluvial regime in this way has management value. In Europe and North America, legislation for river management is based increasingly on ecological considerations, so a thorough understanding of species habitat requirements and habitat-forming processes is needed. Our index is at a scale most often targeted by river managers (that of the habitat unit) and captures the physical controls on spawning habitat availability relatively rapidly. It can be used to set ecological targets or objectives as well as to assess potential ecological response to natural and anthropogenic disturbances that alter stream flow and shear stress patterns. It may also be useful in river restoration initiatives, which often fail because of the lack of explicit links between fluvial processes and biota (Wohl et al. 2005).

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List of symbols used in the text and their definitions

Symbol Definition

D_{50}	median size of spawning sediment, 41.1 mm in this analysis
d_{c50}	critical depth for incipient motion of spawning sediment, $\tau_{c50}/\rho_w g S$
g	gravitational acceleration
n	Manning's roughness coefficient
R	hydraulic radius
S	channel slope

v_{c50}	critical velocity for incipient motion of spawning sediment determined from the Manning equation, $d_{c50}^{0.67} S^{0.5}/n$
ρ_s	sediment density, 2650 kg·m ⁻³
ρ_w	water density, 1000 kg·m ⁻³
τ_{xs}	excess bank-full shear stress, $\tau - \tau_{c50}$
τ	shear stress determined from the depth–slope product, $\rho_w R g S$, evaluated at bank-full flow
τ_{c50}	critical shear stress for incipient motion of spawning sediment, $\tau^*_{c50} g D_{50} (\rho_s - \rho_w)$
τ^*_c	critical Shields parameter for incipient motion, 0.045
Ω	total stream power, $\rho g S Q_{bf}$, where Q_{bf} is bank-full discharge
ω	specific stream power, Ω/w_{bf} , where w_{bf} is bank-full channel width
ω_{xs}	excess specific stream power, $\omega - \omega_{c50}$, evaluated at bank-full flow
ω_{c50}	critical specific stream power for incipient motion of spawning sediment, $v_{c50} \tau_{c50}$