Channel type and salmonid spawning distribution and abundance

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Abstract: Consideration of fundamental channel processes, together with map-based and field investigations, indicates that stream channel type influences salmonid spawning distributions across entire channel networks and salmonid abundance within channel reaches. Our analysis suggests that salmonid spawning patterns in mountain drainage basins of the Pacific Northwest are adapted to, among other things, the timing and depth of channel bed mobility. We hypothesize that because the bed of pool–riffle and plane–bed reaches scours to a variable fraction of the thickness of alluvium, survival to emergence is favored by either burying eggs below the annual scour depth or avoiding egg burial during times of likely bed mobility. Conversely, annual mobility of all available spawning gravel in steeper step–pool and cascade channels favors either adaptations that avoid egg burial during times of likely bed mobility or selection of protected microhabitats. Consistent with these expectations, we find that salmonid spawning distributions track channel slope distributions in several west-slope Pacific Northwest watersheds, implying that spatial differences in channel processes influence community structure in these rainfall-dominated drainage basins. More detailed field surveys confirm that different channel types host differential use by spawning salmonids and reveal finer-scale influences of pool spacing on salmonid abundance.

Résumé : L'examen des processus fondamentaux des chenaux, combiné à des études cartographiques et à des travaux de terrain, montre que le type de chenal influe sur la distribution de la fraye des salmonidés à l'échelle du réseau de chenaux et sur l'abondance des salmonidés dans les tronçons des chenaux. Notre analyse permet de penser que les profils de fraye des salmonidés dans les bassins versants montagneux de la côte nord-ouest du Pacifique sont adaptés, entre autres, aux caractéristiques temporelles de la mobilité du lit des chenaux et à l'épaisseur de la couche concernée. Nous avançons l'hypothèse qu'étant donné que l'affouillement du lit des tronçons constitués de fosses et de rapides et des tronçons à lit plat touche une fraction variable de la couche d'alluvions, la survie jusqu'à l'émergence se trouve favorisée si les oeufs sont enfouis au-dessous du niveau d'affouillement ou si les femelles évitent d'enfouir leurs oeufs durant les périodes où le lit risque d'être affouillé. Par ailleurs, la mobilité annuelle de l'ensemble du gravier de fraye disponible dans les chenaux à pente prononcée constitués de seuils et de fosses et dans les cascades favorise soit les adaptations qui font que les femelles évitent d'enfouir leurs oeufs durant les périodes de mobilité probable du lit, soit le choix de microhabitats protégés. Conformément à ces observations, nous avons trouvé que les distributions de la fraye des salmonidés reflètent les distributions des chenaux selon leur pente dans plusieurs bassins du versant ouest de la côte nord-ouest du Pacifique, ce qui implique que les différences spatiales dans les processus des chenaux influent sur la structure des communautés dans ces bassins versants qui reçoivent d'importantes précipitations. Des études de terrain plus détaillées confirment que les différents types de chenaux suscitent des utilisations différentes par les salmonidés dans la période de reproduction et révèlent l'existence d'effets à plus petite échelle de l'espacement des fosses sur l'abondance des salmonidés.

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Introduction

Traditional explanations offered for controls on the timing and distribution of spawning among and within species invoke biological factors such as competition, egg size, prey availability, and body size (Chapman 1966; Gorman and Karr 1978; Moyle and Vondracek 1985; Beacham and Murray 1987) and physical influences such as intergravel flow, substrate size, and stream temperature (Stuart 1953; Schlosser 1985; Brannon 1987; Matthews 1987; Poff and Ward 1990). Although it is widely recognized that disturbance in general and discharge in particular affect stream fish communities (Horwitz 1978; Resh et al. 1988; Strange et al. 1992), the relationship between geomorphic processes and the phenology of reproduction and early life histories has received little attention.

Salmonids occupy a variety of habitats within the stream network (e.g., Platts 1979; Li et al. 1987), and variation in the spatial and temporal distribution of spawning makes salmonids well suited for testing hypotheses related to the role of physical factors in determining life history traits. Anadromous salmon bury their eggs >20 cm below the channel bed (McNeil 1962; van den Berghe and Gross 1984; Chapman 1988), whereas smaller resident and anadromous trout have shallower egg burial depths, typically on the order of 5–10 cm (Needham 1961; Crisp and Carling 1989; Grost et al. 1991; Knapp and Vredenburg 1996). Larger females are capable of digging deeper redds (van den Berghe and Gross 1984; Crisp and Carling 1989), and egg survival to emergence is inversely related to the depth of scour during the period between spawning and emergence (Holtby and Healey 1986). Based on observations that chum salmon (*Oncorhynchus keta*) bury their eggs just below scour depths during bankfull flow, Montgomery et al. (1996*b*) suggested that egg burial depths represent an adaptation to depths of scour during typical winter storms.

Anadromous and resident species often inhabit different reaches of a channel network and spawn at different times. The usual explanation for spawning site selection is species-specific preferences for depth, velocity, and substrate (Burner 1951; Smith 1973). Spawning timing is typically attributed to synchronization of temperature-specific embryo development rates with seasonal patterns of prey availability for the progeny after they emerge (Beacham and Murray 1987; Brannon 1987). While such adaptations are important, we hypothesize that spawning distribution and timing also reflect the timing of bed mobility and the depth of scour in different portions of a channel network. In support of this hypothesis, we present evidence that fundamental spatial and temporal differences in channel processes influence salmonid spawning distributions and timing in rainfall-dominated drainage basins west of the Cascade crest in the Pacific Northwest (PNW). We further show that subreach-scale geomorphic characteristics also influence salmonid abundance and community composition. The strong association of reach-level channel types and salmonid distributions has important implications for salmonid conservation and watershed restoration efforts in the PNW.

Bed scour hypothesis for salmonid distributions

The hypothesis that bed scour depths constrain salmonid distributions is based on the premise that it is unlikely that a population could persist in an environment where annual scour depths consistently exceeded egg burial depths during the incubation period. In mountain drainage basins, interactions among channel morphology, bed roughness, and sediment transport lead to differences in patterns of scour between different types of channels (Montgomery and Buffington 1997). We hypothesize that such differences constrain the type of fish that could be adapted to different places in the channel network because of the relationship between fish size and egg burial depths. Below, we elaborate on this general hypothesis to lay out specific expectations for PNW channels.

Salmonids typically spawn in gravel- to cobble-sized substrate (e.g., Kondolf and Wolman 1993), and the depth of scour experienced by a redd will reflect differences in both the discharges to which it is exposed and geomorphic context. The frequency of flows associated with significant sediment transport varies for individual channels, but recurrence intervals for bankfull flow generally are on the order of 1–2 years (Williams 1978). Some bed mobility occurs at stages below bankfull (Jackson and Beschta 1982), but widespread bed mobility commonly occurs at a stage near bankfull (Carling 1983; Andrews 1984). Steep and low-gradient channels, however, fundamentally differ in the extent of bed mobility and the depth of scour during typical bed-mobilizing events.

Low-gradient reaches of mountain drainage basins generally exhibit gravel-bedded pool–riffle, forced pool – riffle, and plane–bed channel morphologies (Leopold et al. 1964; Church 1992; Montgomery and Buffington 1997). The bed of pool–riffle channels consists of the classic laterally oscillating sequence of bars, pools, and riffles. In contrast, plane–bed channels are characterized by a relatively featureless bed, and forced pool – riffle channels are those in which the majority of bars and pools are linked to local hydraulic convergence or divergence arising from local flow obstructions, such as large woody debris. Most of the bed-forming material within these channels may be suitable for spawning, and the full thickness of alluvium beneath the channel bed is rarely mobilized. Bankfull flows generally mobilize the streambed across the entire channel, and the average thickness of the layer in active transport, which sets the depth of scour, can be related to the rate of bedload transport (Carling 1987), although bedload transport and the associated scour depth can vary greatly across a channel during a single event (Hassan 1990). The bedload transport rate, in turn, is determined by the peak discharge's magnitude and duration (Milhous 1973; Jackson and Beschta 1982; Sidle 1988), which may vary dramatically from year to year, and the grain size of the bed-surface sediment, which may respond to changes in sediment supply (Dietrich et al. 1989). Increased sediment transport as a result of either higher discharges or greater sediment supply should increase the average depth of scour in low-gradient (i.e., pool–riffle and plane–bed) channels.

Steep alluvial channels tend to exhibit either step–pool or cascade morphologies. Step–pool reaches consist of large clasts organized into discrete channel-spanning accumulations that form a series of steps between pools containing finer material (Grant et al. 1990; Church 1992; Montgomery and Buffington 1997). In contrast, cascade channels are characterized by longitudinally and laterally disorganized accumulations of coarse bed material. Potential spawning gravel in step–pool or cascade channels typically occurs only locally in pools, the lee of large clasts, or other hydraulically sheltered locations. The stepped morphology and large grain sizes relative to the size of bedload material imply a high relative transport capacity (Montgomery and Buffington 1997). In contrast with lower-gradient channels, bedload transport in step–pool and cascade channels exhibits dual-threshold mobility, as large bed-forming clasts remain stable at discharges that mobilize gravel-sized material. Sediment transport rates in step–pool and cascade channels primarily reflect the availability of readily transportable sediment, and gravel-sized material is more frequently mo-

Table 1. Hypothesized constraints on salmonids with different depths of egg burial relative to annual scour depths.

Spawning season	Egg burial depth (EB) versus scour depth (SC)	Rain-dominated low-gradient channels	Rain-dominated steep channels	Snow-dominated low-gradient channels	Snow-dominated steep channels
Spring	EB > SC	Possible	Possible	Possible	Precluded
Spring	EB < SC	Possible	Possible	Precluded	Precluded
Fall	EB > SC	Possible	Precluded	Possible	Possible
Fall	EB < SC	Precluded	Precluded	Possible	Possible

bile than coarser step-forming clasts (see review by Montgomery and Buffington 1997). During events that mobilize the between-step portions of the bed, active transport scours virtually the full depth of the gravel that could provide spawning habitat. Hence, there is a very high probability of mortality to buried eggs even during relatively common high flows.

We hypothesize that the fundamental difference in the mobility of potential spawning gravel in steep and low-gradient channel types described above constrains the potentially successful combinations of spawning timing and egg burial depths in mountain channel networks. In low-gradient channels where the active transport layer consists of a portion of the gravel thickness, two spawning strategies should be viable: (*i*) avoidance of egg burial in the gravel during the most likely time of bed mobility or (*ii*) burying eggs below the average annual scour depth. In contrast, avoidance of egg burial during times of likely bed mobility should be the only viable strategy in steep channels, where the active transport layer consists of the full thickness of potential spawning gravel.

In the PNW, the most probable time for annual high flows depends on whether runoff is rain dominated or snowmelt dominated. High flows in rain-dominated watersheds generally occur in winter, whereas high flows in snowmelt-dominated watersheds generally occur in spring. These differences lead to the expectation of spatial differences in the distribution of spring and fall spawning for salmonids in snowmelt-dominated and rainfall-dominated channels. A bed mobility control on spawning timing and egg burial depths predicts that in rain-dominated drainage basins, (*i*) fall spawning is not likely to be very successful (i.e., prevalent) in steep channels, (*ii*) fall spawning may be successful in lower-gradient channels if eggs are buried deeper than the average depth of scour, and (*iii*) spring spawning should be viable throughout the channel network.

Under the assumption that large fish can bury eggs beneath the annual scour depth and that small fish cannot, the constraints predicted by a bed mobility control on salmonid spawning can be summarized as follows for PNW channels (Table 1). Fall spawning in low-gradient channels should be viable only for large fish. In contrast, small salmonids could only spawn in spring, but could use both steep and low-gradient channels. The bed scour hypothesis further predicts that in snowmelt-dominated basins with annual high flows consistently in spring, the only fish that could spawn in low-gradient channels during spring would be large fish and that spring-spawning fish of any size would be severely disadvantaged in steep channels. Conversely, there would be no constraint on the distribution of fall-spawning fish; they could use the entire channel network. In contrast with basins with predictable annual high flows, basins in which annual high flows occur in either spring or fall (e.g., rain-on-snow dominated basins) would not be expected to have as significant a bed mobility influence on spawning distributions or timing.

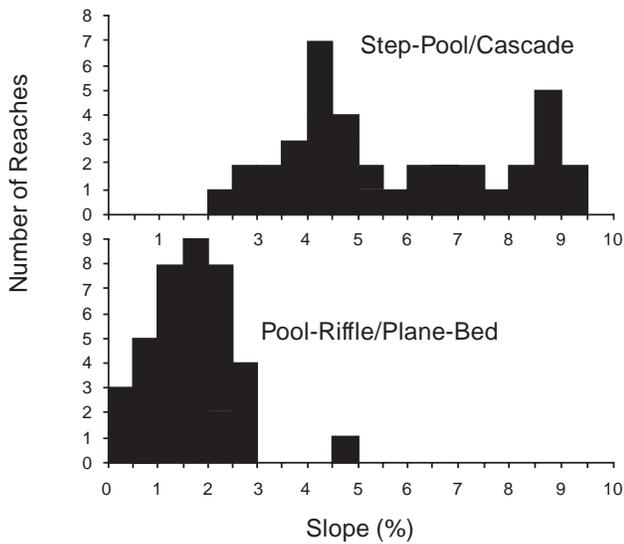## Networkwide spawning distributions

In our multiscale investigation of geomorphic influences on salmonid spawning and abundance, we first examine the relationship between networkwide spawning distributions and channel types inferred from map-based analysis to provide an initial test of the hypothesized bed scour control on spawning distributions. Second, we analyze field surveys of spawner abundance in different channel types to investigate specific relationships between fish use and channel type. Finally, we analyze within-reach surveys to examine the degree to which subreach-scale variations in pool spacing influence salmonid abundance.

Our analysis of networkwide spawning distributions examines locations where data for spawning distributions were available from watersheds with a variety of channel types. This initial test of our hypothesis focuses on watersheds with rain-dominated hydrographs because (*i*) the potential for rain-on-snow events to produce high flow in many snowmelt-dominated basins would influence the predictability of the time of annual high flows and (*ii*) data available to us were from watersheds to the west of the crest of the Cascade Range.

Methods

Our test of predicted spawning distributions used data from the Clearwater River and portions of the Stillaguamish River basin in western Washington and from the Applegate River in southern Oregon. The 384-km^2 Clearwater River on the Olympic Peninsula, Washington, is ideal for testing our hypothesis because the basin had an extensive survey of spawning populations and fish distributions conducted in the early 1970's prior to intensive logging in the watershed (Edie 1975). Squire Creek is a 68-km^2 tributary that drains into the North Fork Stillaguamish River on the western slope of the Cascade Range in northern Washington. The basin consists of low-gradient channels that flow across the floodplain of the North Fork Stillaguamish River and steeper channels that emerge from bedrock-walled valleys. Squire Creek has no known barriers to fish migration, and spawner surveys have been conducted since 1974. The Applegate River watershed is an approximately 1970-km^2 drainage basin in the southern Oregon Coast Range, although its headwaters extend into northern California. The extent of the channel network used by different species of fish was summarized in a series of figures in the Applegate watershed assessment (Applegate River Watershed Council 1994).

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Fig. 1. Histogram of reach – average slopes for channels surveyed in field studies in western Washington State.

**Fig. 2.** Maps of the Clearwater River drainage basin on the Olympic Peninsula, Washington, showing (A) fish distribution zones defined by Edie (1975) (black bars across channels represent mapped fish passage barriers) and (B) channel gradients derived from U.S. Geological Survey 7.5′ topographic quadrangles. S, slope.

Together, these three basins allow a regionwide evaluation of predicted versus observed zones of fish use within mountain drainage basins.

In each of the watersheds for which maps of fish use were available, we measured channel gradients from U.S. Geological Survey 7.5′ topographic quadrangles. Channel gradients were determined by dividing the contour interval (typically 40′ or 12 m) by the distance between successive contours. Field measurements from previous studies of PNW channels indicate that pool–riffle and plane–bed reaches typically have gradients <3%, whereas step–pool and cascade reaches typically have gradients >3% (Fig. 1). Within the low-gradient channels, plane–bed and forced pool – riffle reaches typically occur on slope of 1–3%; channels with slopes ≤1% typically exhibit pool–riffle morphologies (Montgomery et al. 1995). Although most of the reaches that we have surveyed in various studies in the region conform to these general expectations, these slope categories are not absolute and channels with these morphologies do occur outside these typical slope ranges (Montgomery and Buffington 1997). Also, previous comparisons of channel slopes derived from field surveys and from 7.5′ topographic maps found that predicted gradients could be in error by as much as ±100%, in spite of an overall correspondence between map-derived and field-surveyed slopes (Montgomery et al. 1998). Channel gradients were used to classify the depicted channel networks into the general categories of low-gradient (<3%) and steep-gradient (>3%) reaches and to further subdivide the low-gradient channels in the Clearwater River and Squire Creek basins into <1 and 1–3% gradient reaches. We then compared the distribution of fish use with the gradient ranges predicted to be suitable for spawning by the bed scour hypothesis, as summarized in Table 1.

Results

Edie's (1975) map of fish distributions based on presence/absence surveys in the Clearwater River basin shows that large, fall-spawning chinook (*Oncorhynchus tshawytscha*) and coho salmon (*Oncorhynchus kisutch*) spawn in major
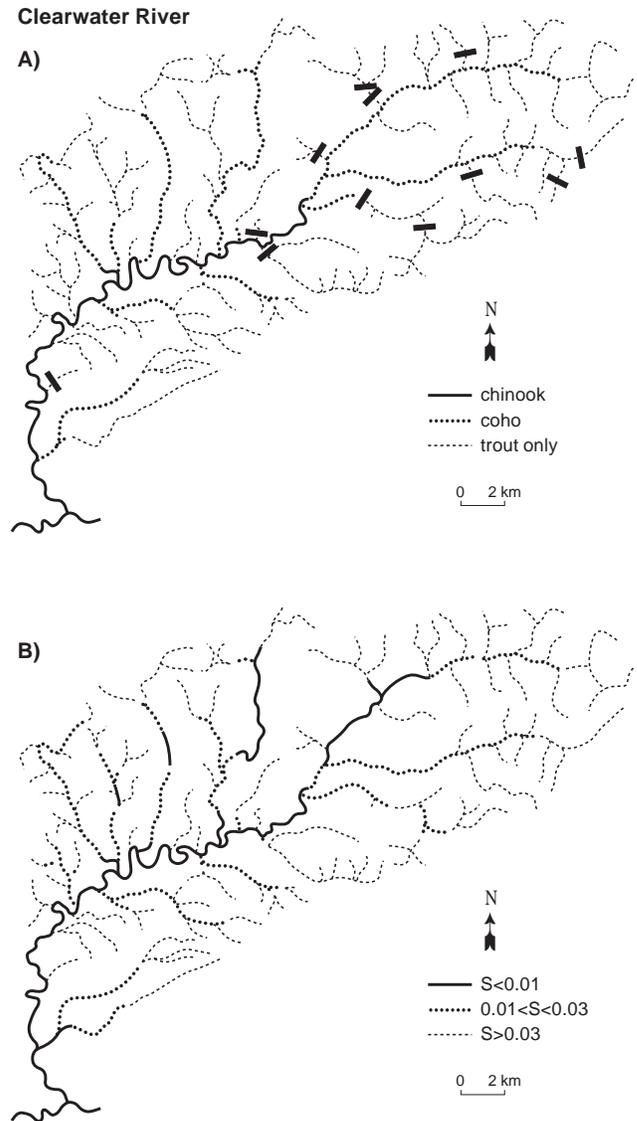
channels, whereas small, spring-spawning cutthroat trout (*Oncorhynchus clarki*) spawn in headwater channels. Large, spring-spawning steelhead trout (*Oncorhynchus mykiss*) occur throughout the network below migration barriers. The salmon and cutthroat trout distributions mirror the distribution of gradient ranges typical for different channel types (Fig. 2). Throughout the basin, the cutthroat-trout-only zone correlates with reaches with slopes >3%, the chinook zone correlates with reaches with slopes <1%, and the coho zone correlates with reaches with slopes of 1–3%. The general correspondence between fish distributions and channel slope supports our hypothesis for a fundamental geomorphic influence on salmonid spawning distributions because steep (i.e., >0.03) reaches in rain-dominated systems should not support fall-spawning salmonids (Table 1).

Table 2. Percentage of total stream length identified in surveys within combinations of fish use zones and channel gradient.

	Channel gradient				% of fish distributed in predicted range
	<0.01	0.01–0.03	<0.03	>0.03	
Clearwater River					
Chinook zone	14	<1		0	100
Coho zone	6	17		1	95
Trout-only zone	<1	9		51	83
Stillaguamish River					
Chinook and coho zone			74	0	100
Trout-only zone			1	24	95
Applegate River watershed					
Chinook and coho zone			54	2	96
Trout only zone			2	42	95

Fig. 3. Maps of the Squire Creek drainage basin in the northern Cascades, Washington, showing (A) fish distributions defined from field surveys and (B) channel gradients derived from U.S. Geological Survey 7.5′ topographic quadrangles.
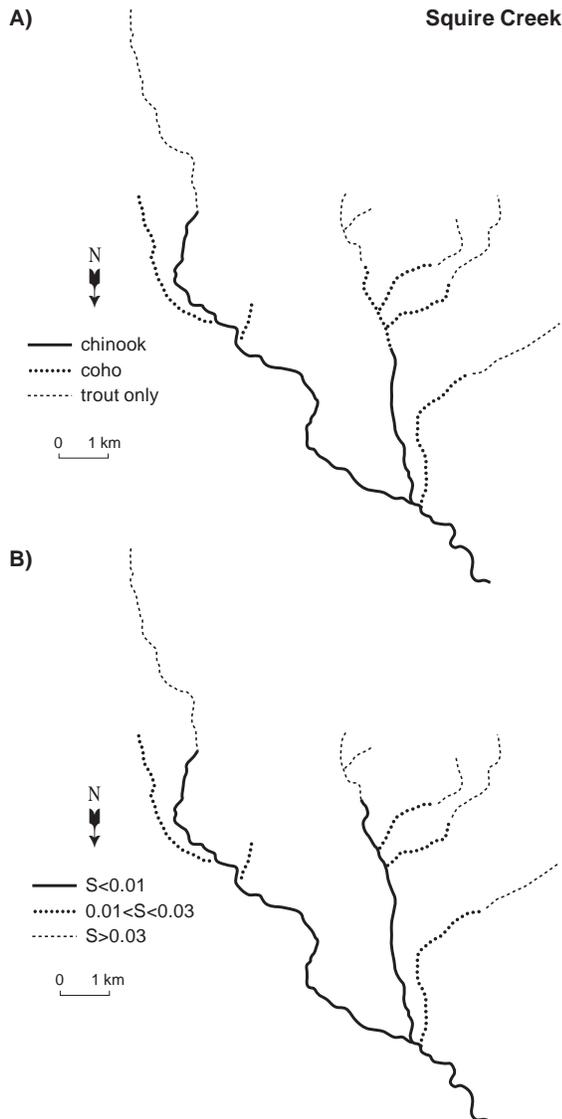
A more quantitative examination of the correspondence of fish distributions and channel type further supports the predictions outlined in Table 1. Almost all of the 15% of the total channel length in the chinook zone is composed of channels with gradients <0.01 (Table 2). Similarly, the 52% of the total stream length composed of reaches with slopes >0.03 concides with the trout-only zone. In total, 100 and 95%, respectively, of the stream length in the chinook and coho zones occurred in the slope range typical for the channel types that the bed scour hypothesis predicts would be hospitable for large, fall-spawning species. Moreover, 83% of the mapped trout-only zone corresponds to the steeper channels, as also predicted by our hypothesis. Superimposed upon these basic patterns of species distributions are access limits imposed by debris jams and waterfalls or other migration barriers. These additional constraints improve the spatial correspondence between observed and predicted patterns of spawning.

In Squire Creek, chinook and coho use only the lower-gradient channels, and the trout-only zone occupies steeper channels (Fig. 3; Table 2). Spring-spawning cutthroat trout also use some lower-gradient channels, and steelhead spawn throughout the basin.

In the Applegate River, anadromous fish use the mainstem river and some of the primary tributary channels, whereas only trout use the smaller headwater channels (Fig. 4). Neglecting the reaches upstream of a dam that blocks anadromous fish from the basin headwaters, there is an excellent correspondence between fish use patterns and channel gradient (Table 2); over 95% of both of the fall-spawning anadromous and trout-only zones in this watershed consisted of channels in the gradient class predicted by our hypothesis. As in the Clearwater River, spring-spawning resident trout occur throughout the basin. Hence, in each of the three study basins, salmonid spawning distributions conform to the expectations of the bed scour hypothesis outlined in Table 1.

Reach-level channel type and fish abundance

Our analysis of field surveys of spawner abundance in different channel types focused on data collected in the Skagit and Stillaguamish rivers, in the northern Cascades, Washington. These surveys provided an additional quantitative field

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Fig. 4. Maps of the Applegate River drainage basin in the Oregon Coast Range showing (A) fish distributions reported in a watershed assessment (black bar across channel represents a dam that blocks anadromous fish passage) and (B) channel gradients derived from U.S. Geological Survey 7.5′ topographic quadrangles. S, slope.

A)

Applegate River

N

—— coho/chinook
······· trout only

0   10 km

B)

N

—— S<0.03
······· S>0.03

0   10 km
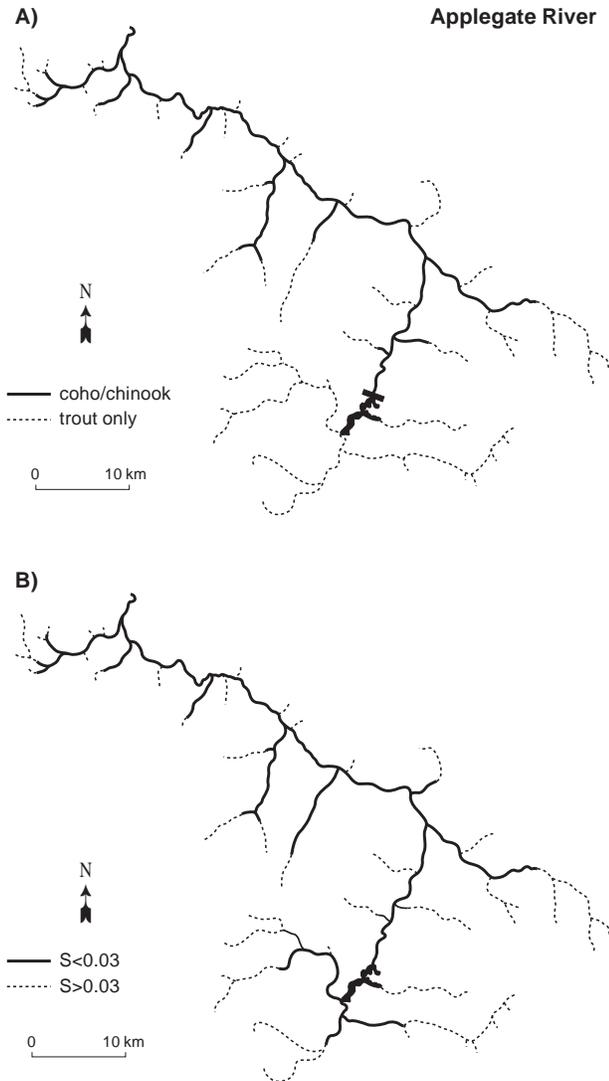
test of the influence of channel type on spawning activity. In particular, these data allow closer examination of fish use patterns and abundance within the lower-gradient channels in the chinook and coho zones.

Methods

In the Stillaguamish River, we used data from repeated surveys of chinook redds and spawning coho conducted by the Washington Department of Fish and Wildlife over 2–23 years. We visited these reaches and classified each as pool–riffle, forced pool – riffle, plane–bed, or step–pool morphology following Montgomery and Buffington (1997). Mean and standard deviations for redds per kilometre and peak fish per kilometre were calculated for each reach. In the Skagit River, we used 50 reach-level surveys of chinook redds conducted in five tributaries to the Skagit River be-

tween 1991 and 1996, with several reaches being surveyed annually between 1994 and 1996. We also used 26 reach-level surveys of spawning coho. As for the Stillaguamish River, we visually classified the surveyed reaches into pool–riffle, forced pool – riffle, plane–bed, and step–pool morphology.

Our analysis of subreach-scale geomorphic influences on fish distribution and abundance focused on pool frequency data collected in the habitat surveys in the Skagit River. The spacing between pools is a fundamental channel attribute that varies widely in forest channels both between channel types and in response to the abundance of coarse woody debris that can force pool formation (Montgomery et al. 1995). Geomorphologists traditionally describe pool spacing in terms of the average length of channel between pools, expressed as the equivalent number of channel widths and termed channel widths per pool. For a given channel reach, a low pool spacing indicates many, closely spaced pools, whereas a high pool spacing indicates few, widely spaced pools.

Results

In records that extend over 2–23 years for the Stillaguamish River, the number of chinook salmon redds and spawning coho salmon per kilometre of channel varied with different channel types (Table 3). The density of chinook spawning varied dramatically by channel type, but similar types of channels exhibited similar redd densities. Redd densities within individual reaches were quite variable, but the mean values for pool–riffle channels ranged from 4.2 to 16.3 redds/km. These mean redd densities are very similar to the range of mean values of 2.5–13.8 redds/km for forced pool – riffle channels. In contrast, no spawning was recorded in plane–bed channels, although they occur in the same gradient range as the forced pool – riffle channels.

In the Stillaguamish River, the peak density of coho spawning also varied systematically by channel type (Table 3). Mean values ranged from 26.3 to 145.9 fish/km in pool–riffle channels and from 173.5 to 281.5 fish/km in forced pool – riffle channels. In contrast with chinook, plane–bed channels did support spawning coho, but at lower densities (8.0–37.9 fish/km). The consistent patterns of fish use over many years indicate channel-type-dependent differences in spawning use within the low-gradient channels usable by large fall-spawning fish in the Stillaguamish River; chinook and coho abundance was highest in forced pool – riffle channels and low in plane–bed channels.

Fish abundance data from the Skagit River revealed similarly strong relationships between channel type and fish use (Fig. 5A). Mean values of spawning density for pool–riffle and forced pool – riffle channels were 33.9 and 31.1 redds/km, respectively. The ranges in spawning use for pool–riffle and forced pool – riffle channels were also very similar. In contrast, the mean spawning density for plane–bed channels was only 2.0 fish/km. During the entire period of observation, only one chinook redd was observed in step–pool channels surveyed on the Skagit River, documenting the very low usage of these steeper channels predicted by our hypothesis, although the shortness of the reach resulted in an anomalously high value for redds per kilometre.

Table 3. Data on channel type and number of observed salmonid redds for repeated spawner surveys along the North Fork Stillaguamish River, Washington.

	Years of data	Channel type and gradient	Reach length (cm)	Bankfull width (m)	Average redds/km	SD redds/km
Chinook salmon						
North Fork mainstem	2	PR 0.002	2700	70.0	16.3	3.3
North Fork mainstem	20	PR 0.003	6900	75.0	9.6	6.1
North Fork mainstem	20	PR 0.003	5600	60.0	12.0	7.6
Boulder River	16	PR 0.008	3950	20.0	4.2	3.6
Squire Creek	23	PR 0.005	1100	24.3	6.4	10.1
Furland Creek	2	FPR 0.015	800	10.0	13.8	1.4
Ashton Creek	2	FPR 0.010	800	10.0	8.8	3.5
Browns Creek	10	FPR 0.012	600	9.2	2.5	4.6
Brooks Creek	4	PB 0.010	1770	14.5	0.0	0.0
Rollins Creek	6	PB 0.027	532	20.0	0.0	0.0
Dicks Creek	4	PB 0.023	2414	17.0	0.0	0.0
Segelson Creek	2	PB 0.016	1931	12.7	0.0	0.0
Coho salmon						
North Fork mainstem	27	PR 0.003	6900	75.0	43.2	66.9
Boulder River	15	PR 0.008	3950	20.0	26.3	30.2
Squire Creek	20	PR 0.005	1100	24.3	145.9	143.0
Furland Creek	28	FPR 0.015	800	10.0	173.5	206.4
Ashton Creek	34	FPR 0.010	800	10.0	273.5	229.4
Browns Creek	36	FPR 0.012	600	9.2	281.5	210.1
Brooks Creek	3	PB 0.010	1770	14.5	37.9	44.5
Rollins Creek	7	PB 0.027	532	20.0	11.4	16.1
Dicks Creek	2	PB 0.023	2414	17.0	8.0	5.6
Segelson Creek	7	PB 0.016	1931	12.7	12.8	21.0

Note: PR, pool–riffle; FPR, forced pool – riffle; PB, plane–bed.

The difference in spawning use between channel types was even stronger for coho salmon in Skagit River tributaries (Fig. 5B). Mean values of spawning density in pool–riffle and forced pool – riffle channels were 110.9 and 101.0 redds/km, respectively, whereas the mean spawning density in plane–bed channels was 2.6 redds/km. No spawning coho were observed in step–pool reaches in the Skagit River tributaries. The consistent differences in these two watersheds revealed a strong association between spawning use and channel type.

Additional field surveys that used electroshocking and snorkeling techniques confirmed the presence of resident trout in the steeper channels that defined the "trout-only zone" in the Skagit and Stillaguamish watersheds. Several studies in the PNW have documented that native trout tend to remain close to their spawning areas (e.g., June 1981; Moore and Gregory 1988), implying that the distribution of juvenile fish closely reflects the species spawning distribution.

Spawning abundance of both chinook and coho in the Skagit River tributaries was inversely related to pool spacing (Fig. 6). Both pool–riffle and forced pool – riffle channels have pool spacings below the traditionally expected five to seven channel widths and have far greater redd abundance than the plane–bed channels. The pool spacing of more than five channel widths for plane–bed channels is consistent with other data for PNW channels (Montgomery et al. 1995). The uniformly low redd abundance (i.e., <20 redds/km) for both chinook and coho indicates lower salmonid abundance in plane–bed channels than in pool–riffle or
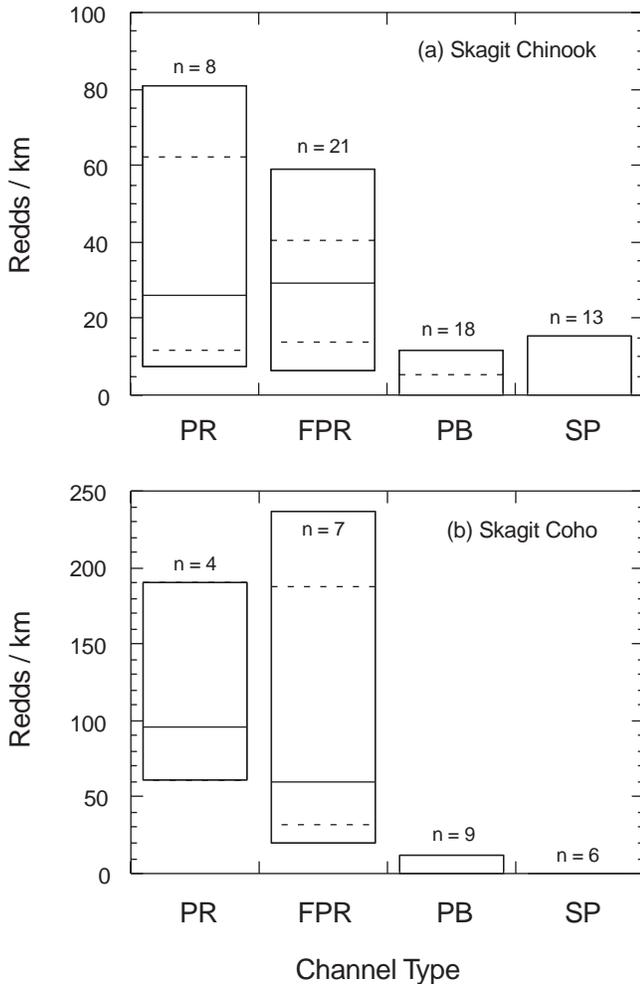
forced pool – riffle channels. Moreover, the strong inverse relationship documents that both of these species have a distinct preference for spawning in reaches characterized by abundant pools.

Discussion

Our data and analyses reveal strong linkages between channel processes and fish use and abundance across a wide range of scales. The general correspondence of spawning distributions across mountain channel networks to those predicted by a simple hypothesis based on streambed scour implies a fundamental geomorphic forcing on broad patterns of salmonid distribution within PNW watersheds. At finer scales, specific habitat attributes appear to influence relative fish abundance and community composition within channel reaches. While we recognize that biological factors influence fish use and abundance across all of these scales, we nonetheless see a large role for channel processes at each scale.

The correlation of spawner abundance with channel type supports our overall hypothesis, but we do not discount stream temperature and microhabitat use (e.g., gravel size, depth, velocity) as important factors affecting the distribution and timing of salmonid spawning. Instead, genetic adaptations to temperature and behavioral responses to habitat may be superimposed on larger patterns controlled by bed mobility and discharge predictability. In some cases, stream temperature may adjust spawning timing by a matter of weeks, but bed mobility may dictate spawning season. In other cases, stream temperature may control spawning tim-

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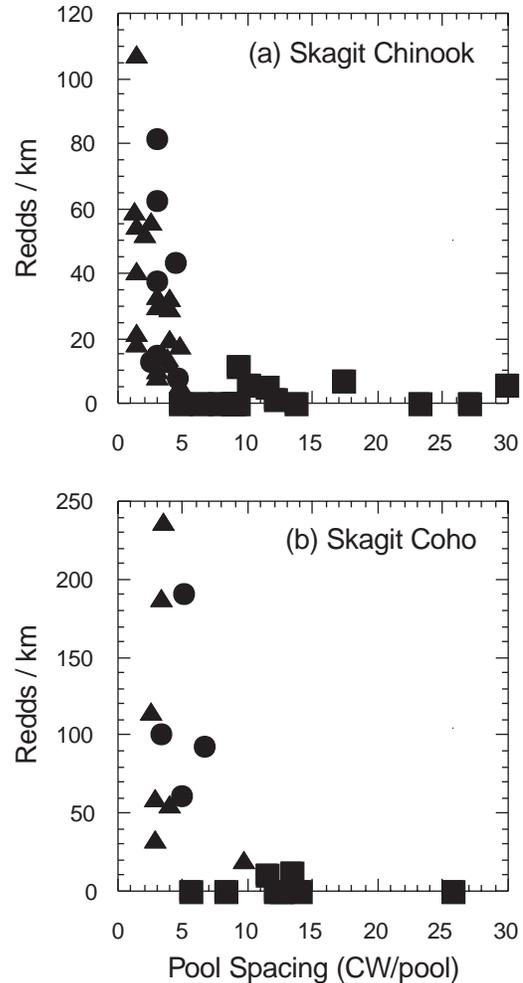Can. J. Fish. Aquat. Sci. Vol. 56, 1999

Fig. 5. Percentile plots of redds per kilometre of stream length by channel type for (A) chinook and (B) coho salmon in tributaries of the Skagit River, Washington. Solid lines within boxes are median values, broken lines are inner and outer quartiles, tops and bottoms of boxes are the 10th and 90th percentiles, and *n* values are the number of sample reaches in each distribution. PR, pool–riffle; FPR, forced pool – riffle; PB, plane–bed; SP, step–pool.

Fig. 6. Redds per kilometre of stream length versus pool spacing (average length of channel between pools in units of channel width (CW) per pool) for (A) chinook and (B) coho salmon in tributaries of the Skagit River, Washington. Squares represent plane–bed reaches, triangles represent forced pool – riffle channels, and circles represent pool–riffle channels.

ing, and annual differences in bed scour may simply influence the abundance of different age classes. In other words, the influence of temperature, flow conditions, and streambed scour may be more or less important in different circumstances.

We would expect that spawning success may have a greater stochastic component where the seasonal timing of high flows has substantial variability. Consequently, we expect bed mobility to be most relevant in environments with predictable hydrologic regimes and spatially variable channel types. Such conditions are likely to characterize mountain drainage basins in humid-temperate environments; the proposed bed scour mechanism may be less important in areas with uniform channel types or unpredictable hydrologic regimes. Furthermore, we would expect the temperature regime to be more important in mountain drainage basins with more extreme ranges in temperature than our study basins, such as in basins in the continental interior.

We are aware of apparent exceptions to our hypothesis that upon closer inspection reflect the influence of other important processes or controls. Microhabitat selection, for example, may influence spawning success through use of hydraulically sheltered locations with relatively stable gravel (e.g., Knapp and Vredenburg 1996). Similarly, sediment impounded behind log jams may decrease local channel gradients enough to alter channel type, and hence fish use, over long stretches of stream channel (Montgomery et al. 1996*a*). In addition, fine-scale stretches of low-gradient channel types (such as forced pool – riffle reaches) can occur within generally steep headwater valleys, and these areas may provide local habitats. Spawning in such localized areas may allow species to successfully occupy portions of a channel network that would otherwise be inhospitable. Conversely, elimination of favorable microhabitat may decimate local populations that rely on such areas in steep mountain streams. The prevalence of side channel spawning along some channel reaches also provides the potential for apparent exceptions to our hypothesis, as side channels should not

scour to depths comparable with the main channel and can thereby present safe spawning environments for small fish. Such factors may be more or less important in particular stream systems. Hence, not every apparent exception falsifies the basic hypothesis regarding scour depths and spawning distributions, which is best viewed as one of many conceptual frameworks within which to test and explore large-scale controls on spawning distribution and timing.

Several workers report that the occurrence of bed-mobilizing events in both fall and spring facilitates the co-existence of spring- and fall-spawning trout in steep Sierran channels (e.g., Seegrest and Gard 1972; Kondolf et al. 1991). Moreover, both spring- and fall-spawning species of trout are present in some steep channels of the Cascade Range that experience both large winter rainstorms and significant springtime snowmelt. The presence of both spring- and fall-spawning trout in these steep channels suggests that unpredictable disturbance timing may prevent exclusion of either spawning population. Despite general consistency between these examples and our hypothesis, further tests and experimentation are needed to refine the regional relevance of our hypothesis, the influence of local hydraulically sheltered environments on exceptions, and the geography of its importance relative to other factors that influence the reproductive success of salmonids.

Implications for conservation

Correlation of fish abundance and channel type could allow for more direct linkages between assessment of channel morphology, habitat quality, and species use and abundance. Chinook and coho abundances are high in pool–riffle and forced pool – riffle channels and are low in plane–bed and step–pool channels. Also, the inverse correlations between anadromous fish abundance and pool spacing imply that dramatic changes in salmonid abundance would follow changes in pool frequency or channel type. As forced pool – riffle and plane–bed channels can both occur within the 1–3% gradient class (Montgomery et al. 1995), this implies that loss of wood debris from a forced pool – riffle channel, and that results in its conversion into a plane–bed morphology (Montgomery and Buffington 1997), will be accompanied by a local decrease in salmon abundance. Addition of simple morphological distinctions appears to hold great potential for increasing the relevance and utility of much of the stream habitat information collected in the mountainous PNW. Considered broadly, the association of channel type and salmonid distributions and abundance provides a framework within which to investigate and interpret population response to changes in sediment supply, discharge regime, or large woody debris.

Our interpretations also imply that changes in scour depths in low-gradient channels should preferentially impact certain species of salmonids. Fall-spawning populations (e.g., chum and coho) in coastal rain-dominated channel systems should be very sensitive to changes in bed scour depths, whereas spring-spawning populations (e.g., cutthroat trout) in these systems should be less sensitive to enhanced scour from increased sediment supply. Considered in this context, the recent dramatic reduction in mean body size of many salmon populations (Bigler et al. 1996) is cause for concern. Not only would smaller females have lower fecundity (Beacham and Murray 1993), but they would also dig shallower, more scour-prone redds.

Conclusions

Salmonid spawning distributions and reproductive success reflect a complicated interplay of biological and physical processes, and our findings emphasize the multiscale influence of geomorphic processes on salmonid abundance. At the scale of entire river networks, differences in bed mobility appear to influence salmonid distributions and spawning timing. Channel types defined by bed morphology appear to explain broad patterns of anadromous and resident species distributions and correlate with spawning densities of different species. Variations in within-reach habitat characteristics also affect the relative abundance of anadromous salmonids. Although our results imply that fundamental physical constraints help set patterns of salmonid use throughout mountain drainage basins, the relative importance of the effects of physical and biological factors on salmonid distribution and spawning timing is likely to vary both locally and regionally. Although other processes may dominate spawning timing in systems with temperature ranges beyond a species' tolerance (or, for example, in spring-fed channels with a uniform flow regime and infrequent bed mobility), we conclude that there is strong, multiscale influence of geomorphological processes on salmonid distribution and abundance in PNW channels.

Acknowledgements

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