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The Relationships among In-Channel Sediment Storage, Pool Depth, and Summer Survival of Juvenile Salmonids in Oregon Coast Range Streams

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Abstract.—The influence of channel aggradation on water availability and salmonid survival was investigated during the summer dry season in two Oregon Coast Range streams. Deep pools and a deformable streambed of coarse gravel were present in highly aggraded stream reaches. However, these thick, highly porous alluvial deposits caused surface flow to become intermittent, which stranded fish in drying channels. In gravel-bed reaches with thinner alluvial deposits, pool depth was limited by the underlying bedrock, but pools were sustained by hyporheic flow throughout the summer dry season. In these moderately aggraded reaches, pool depth and area decreased throughout the summer, resulting in severe crowding of fish trapped in pools formed over small patches of exposed bedrock and isolated by dry, gravel-bed riffles. Bedrock-dominated stream reaches had slightly smaller pools but were most likely to contain continuous surface flow throughout the summer dry season; these reaches exhibited the smallest decreases in pool depth and area. Repeated snorkel surveys indicated that fish abundance in pools decreased by 59% during the summer, significantly higher losses occurring in gravel-bed pools. Streambed substrate and partitioning of surface and subsurface flow may also have important implications for fish energetics due to differences in water temperature and food availability.

Stream channels in mountainous terrain can progressively build up (aggrade) or erode (degrade) the streambed in response to changes in sediment supply (Lisle 1982) or hydraulic controls such as large, in-stream wood (Nakamura and Swanson 1993; Montgomery et al. 1996; Buffington and Montgomery 1999). These processes are important to natural resource and fisheries managers, in part because: (1) land-use practices and wildfires, particularly preceding large storms, can be associated with massive inputs of sediment to stream channels (Swanson 1981; Madej and Ozaki 1996; Benda and Dunne 1997a; May and Gresswell 2003), and (2) the condition of stream channels may strongly affect the population viability of highly valued endangered species, such as coho salmon *Oncorhynchus kisutch*.

Although many studies have investigated the direct effects of fine sediment on the habitat and physiology of salmonids (e.g., Cooper 1965; Beschta and Jackson 1979; Tappel and Bjornn 1983; Lisle 1989; Lake and Hinch 1999), the effects of coarse sediment inputs have not been established. Many of the effects of fine sediment occur only during the egg-to-fry-emergence stage or when fine sediment is suspended in water during periods of high stream discharge. Because fluxes of coarse sediment can change the overall morphology of the channel, their effects are more persistent. Changes in channel morphology caused by large influxes of sediment may be particularly important during periods of extremely low stream discharge, when salmonids face challenging conditions for survival and growth, and during the incubation period, when stable spawning gravels are necessary. Thus, coarse sediment dynamics are highly likely to significantly affect population viability.

In the Oregon Coast Range, a large proportion of the channel network in mountainous terrain is susceptible to channel aggradation based on reach-scale transport and storage capacity (Montgomery et al. 2003). In this region, stream channels typically have a thin layer of highly mobile alluvium that is composed primarily of coarse gravel that resides directly over the underlying bedrock. The presence of a bedrock or alluvial reach morphology depends on the balance between local transport capacity and coarse sediment supply (Montgomery et al. 1996). This relationship can be influenced by log jams that trap sediment, local variations in sediment supply, and bedload-clast lithology (Montgomery et al. 1996; Massong and Montgomery 2000). Large influxes of sediment from landslides and debris flows can overwhelm the local transport capacity and can lead to sub-

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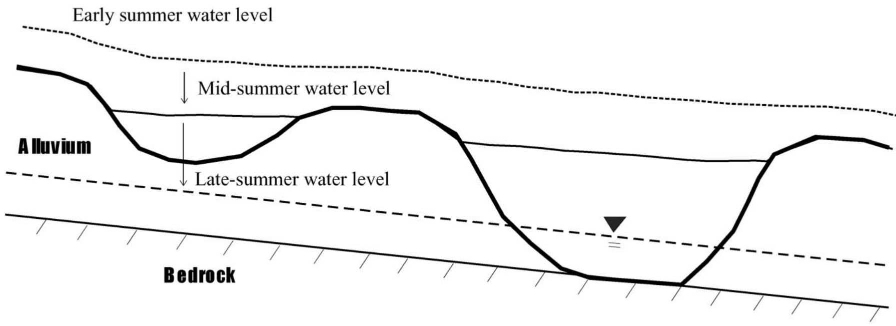

FIGURE 1.—Conceptual diagram of the influence of channel aggradation on water availability during the summer dry season.

stantial aggradation of the channel (Reeves et al. 1995; Benda and Dunne 1997b; Hogan et al. 1998).

Deep pools have the potential to form in aggraded reaches because of a deformable bed created by the stored alluvium. In reaches with less sediment in storage, the underlying bedrock typically limits pool depth (Reeves et al. 1995). Many studies have suggested that large, deep pools create optimal habitat for salmonids (Reeves et al. 1993; McIntosh et al. 1994; Bisson et al. 1997); however, expectations of habitat quality are often based on observations of large numbers of fish occupying deep pools. Such observations may be a misleading indicator of habitat quality because they do not consider how fish survival or growth varies among different pool types.

As an alternative to the conventional view of deep pools, we propose a hypothesis that deep pools formed in areas of thick alluvial deposits have a greater likelihood of going dry during the summer dry season, thereby posing a detriment to fish survival. In deep, highly porous substrates, streamflow levels can drop below the bed elevation during low-flow periods in late summer (Figure 1). This interaction with the hyporheic zone is created by surface water infiltrating through the gravel bed into the interstitial areas in the subsurface. Hyporheic flow eventually returns to the surface of the stream, particularly where patches of bedrock are exposed. There is a growing recognition that the hyporheic zone is an important and dynamic component of aquatic ecosystems (e.g., Hynes 1983; Stanford and Ward 1988, 1993; Findlay 1995; Edwards 1998; Wondzell and Swanson 1999). However, the volume of the hyporheic zone can be greatly increased by changes in sediment supply and retention (Edwards 1998). Alternatively, in areas of low sediment storage, smaller pools may form but these pools may have a higher likelihood of remaining wet throughout the summer because they intercept subsurface flow traveling across the bedrock surface. Patterns of pool drying thus provide a first-order control on fish survival during the summer dry season.

This study had four objectives: (1) to quantify the area and depth of pools in bedrock and aggraded stream reaches, (2) to document which pools persisted throughout the summer dry season, (3) to compare fish survival estimates between bedrock-controlled pools and pools formed in thick deposits of alluvium, and (4) to predict areas susceptible to channel aggradation and pool drying.

Study Basins

The Oregon Coast Range consists of rugged mountains at low elevations (<500 m) that are deeply dissected by an extensive drainage network of steep, V-shaped valleys. The topography is similar to the ridge and ravine topography described by Hack (1960). Landslides and debris flows are important processes in landform development and are dominant mechanisms for routing sediment from hill slopes and headwater streams into mainstem river valleys (Dietrich and Dunne 1978).

Segments of two streams with a mixture of bedrock and alluvial reaches were selected for investigation (Table 1; Figure 2). These sites were selected because they provided examples of channels that experienced recent influxes of coarse sediment and because their disturbance histories were well documented (Reeves et al. 1995; Benda and Dunne 1997a, 1997b; May and Gresswell 2004). Tertiary marine sedimentary rocks of the Tyee Formation (Baldwin 1964) underlie both basins. Harvey Creek, a tributary to the lower Umpqua River, has a history of minimal logging and road construction. Knowles Creek is a tributary to the Siuslaw

TABLE 1.—Channel and basin characteristics of Harvey and Knowles creeks, Oregon.

Variable	Harvey Creek	Knowles Creek
Channel length surveyed (m)	2,990	3,595
Drainage area of surveyed channel (km^2)	8.2–17.8	5.1–19.8
Number of		
Gravel-bed pools	65	18
Gravel pools with bedrock contact	9	22
Bedrock pools	13	26
Gravel-bed glides	7	15
Gravel glides with bedrock contact	0	8
Bedrock glides	2	19

River and is managed for commercial timber production. Two extremely large storms in 1996 triggered more than 20 debris flows in each basin (May 2002; May and Gresswell 2004).

The sandstone lithology of the southern and central Oregon Coast Range produces a unique particle-size distribution. Gravel and sand are the dominant particle sizes, and larger cobbles and boulders are typically limited to discrete patches associated with landslide and debris-flow deposits (Benda 1990). The low abundance of silt and clay produced from this lithology, combined with the loose gravel and sand, produce a highly porous substrate and a strong potential for hyporheic exchange.

The region has a maritime climate characterized by wet, relatively warm winters and dry summers. Average annual precipitation ranges from 165 to 229 cm, falling mostly as winter rain. The summer season is a period of extensive drought that typically persists from June through September. Mean monthly discharge for August at a nearby stream gauge on the undammed Siuslaw River was 4.5 m^3/s for the 26-year period of record. Mean August discharge during the study period (June–August 2002) was 4.1 m^3/s, which is only slightly below average. No increases in streamflow occurred during the sampling period (total June–August precipitation at North Bend Airport was less than 6 mm; National Weather Service, unpublished data).

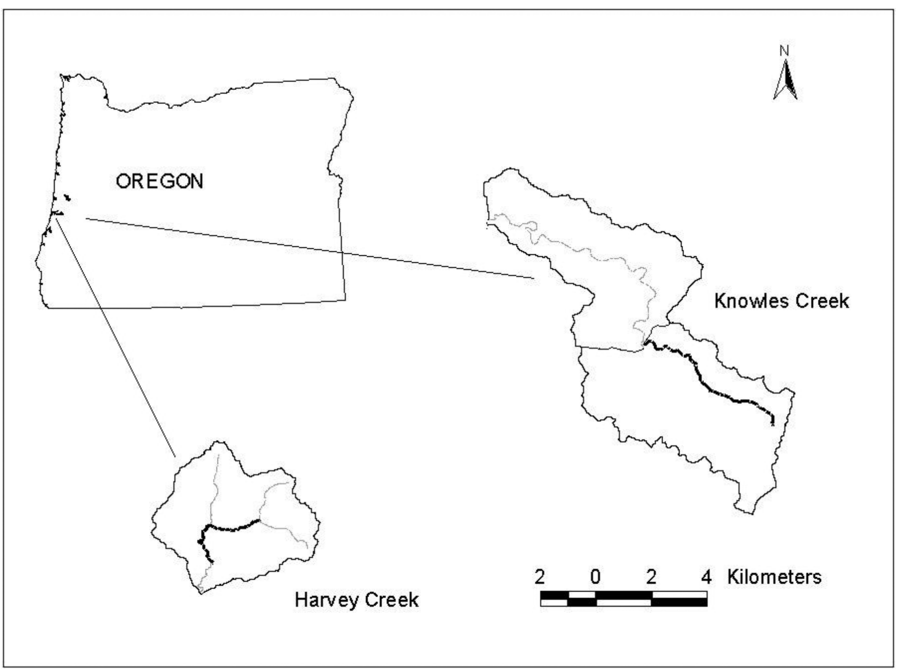

FIGURE 2.—Location of the study basins (Harvey and Knowles creeks) in the Oregon Coast Range, Oregon. Bold lines represent the study reaches.

TABLE 2.—Midsummer (24 June–11 July) and late-summer (25–30 August) connectivity of pools and glides in Harvey and Knowles creeks, Oregon, during 2002. Pools with high connectivity had sufficient streamflow between upstream or downstream riffles to allow fish passage. Low connectivity classifications only considered inflow from upstream in order to assess the potential for invertebrate drift.

Habitat type	Midsummer connectivity			Late-summer connectivity		
	High (%)	Low (%)	None (%)	High (%)	Low (%)	None (%)
Bedrock dominated	83	73	17	5	44	54
Gravel with bedrock contact	76	86	14	2	33	65
Gravel bed	32	37	63	0	1	99

Fish species present during the summer include juvenile coho salmon *Oncorhynchus kisutch*, juvenile steelhead *O. mykiss*, cutthroat trout *O. clarki*, sculpins *Cottus* spp., and dace *Rhinichthys* spp. The dominant forest type is Douglas-fir *Pseudotsuga menziesii* in the uplands; red alder *Alnus rubra* are common in riparian zones.

Methods

Surveys of habitat types and fish abundance were conducted during the dry season in midsummer (24 June–11 July 2002) and late summer (25–30 August 2002). All habitat units within the study area were censused and classified as pools, glides, or riffles (Bisson et al. 1982). Three pool types were identified: (1) pools scoured into alluvium, with no bedrock contact (gravel-bed pools), (2) pools scoured into alluvium, with a bedrock contact at the pool bottom (gravel pools with bedrock contact), and (3) pools formed by bedrock depressions that had little or no alluvium in storage (bedrock pools). Pools included in the survey were at least as long as the bank-full channel width, and at least 30 cm in maximum depth. Glides were classified as low-gradient, shallow (<30-cm maximum depth), homogenous channel units. Glides were similarly classified into three categories of bedrock and alluvial substrates and were included in all analyses except those based on residual pool dimensions. Because habitat classification is a subjective measure, observer bias can seriously compromise the repeatability, precision, and transferability of surveys (Hankin and Reeves 1988; Poole et al. 1997). To increase consistency of the surveys, a single individual, who was highly trained and experienced, classified all habitat units.

Residual pool depth and residual area were measured during midsummer for each pool by use of standard survey equipment and standard protocol (Lisle 1987). Residual depth is defined as the difference in bed elevation between the bottom-most point in a pool and the downstream riffle crest (Lisle 1987). Residual pool depth and area are useful metrics for quantifying pool dimensions because they are independent of discharge. Dimensions of the wetted channel and the maximum pool depth were recorded for each habitat unit during both sampling periods to assess the change in available habitat.

Connectivity to upstream or downstream habitats was documented for each habitat unit. Pools and glides that were completely isolated by dry riffles on the upstream and downstream ends were classified as having no connectivity. Pools and glides with inflow from shallow, upstream riffles that were impassable for fish but that still had the potential to provide a conduit for invertebrate drift were classified as having low connectivity. Pools and glides attached to upstream or downstream riffles that had sufficient flow to allow fish movement were classified as having high connectivity. Two standards were used. In coarse substrate, riffles less than 5 cm deep were considered barriers to fish passage. Coarse substrate provided intermittent pockets of water between individual grains, and no consistent fish passage corridors were apparent in these shallow riffles. For riffles with a bedrock substrate, a minimum of 2 cm of continuous flow was required for passage. This change in criteria was based on our observations of fish passing through extremely shallow riffles with a bedrock substrate where a continuous flow path was present. Because pools or glides with low connectivity on the upstream end could also be classified as having high connectivity on the downstream end, the row sums in Table 2 will not necessarily equal 100%.

The relative abundance of salmonids was estimated by snorkel surveys in each pool and glide during the midsummer and late-summer sampling periods. The midsummer survey was timed to coincide with the period when the majority of pools were becoming isolated, so that fish observed in an individual pool were presumably trapped there for the remainder of the summer. Riffles were usually too shallow for divers and were not included in the surveys. Divers entered each habitat unit at the downstream end and proceeded slowly upstream. All observations of fish were made between 0900 and 1600 hours on days with little or no cloud cover. Divers identified salmonids as either juvenile coho salmon or juvenile trout. Sculpins and dace could not be estimated reliably because they commonly occupied benthic habitats.

Estimates of fish mortality, presumably due to desiccation, were based on the number of fish observed rearing in midsummer pools and glides that were dry by late summer. Mortality estimates were based on two underlying assumptions: (1) physical isolation of pools by midsummer prevented movement of fish among pools, and (2) all fish stranded in dry pools died. Because streamflow did not increase during the sampling period, we assumed that there were no opportunities for movement between isolated pools.

Stream temperature data were collected at 30-min intervals from 26 to 30 August in three pools within a 1-km section of Harvey Creek. We used Onset Stowaway temperature sensors, which have an accuracy of ±0.2°C. Prior to deploying the sensors in the field, we tested them for accuracy in the laboratory. Each sensor was located in a pool with different substrate and streamflow conditions.

Statistical analyses.—One-way analysis of variance (ANOVA) was used to detect significant differences among pool dimensions for each pool type. If a difference was detected, a Kruskal–Wallis multiple comparison procedure was used to identify which groups differed. The influence of residual pool depth on the likelihood of pools remaining wet throughout the summer was tested with the log-likelihood test in logistic regression.

Changes in fish abundance (i.e., survival from midsummer to late summer) and fish density in each pool type were tested by use of ANOVA, followed by a Kruskal–Wallis multiple comparison procedure to detect significant differences among groups. Data from pools that went dry during the summer were omitted from the analysis of fish density in order to assess the degree of crowding in remnant pools that persisted throughout the summer.

The likelihood of stream reaches going dry and the presence of gravel-bed pools were tested with logistic regression. The initial model included four reach-scale and basin-scale variables: (1) basin, (2) longitudinal distance upstream from the mouth of the basin to the headwaters (calculated from 10-m-resolution digital elevation models), (3) recent debris-flow deposits (identified during field surveys), and (4) depositional reaches that plotted below an empirically derived threshold of drainage area and channel slope (predicted by Montgomery et al. 1996). Reach-scale channel gradient was measured in the field with a clinometer, and drainage area was calculated from 10-m-resolution digital elevation models. Variables included in the final model were selected by the probability level of the parameter (those with $P < 0.05$ were included).

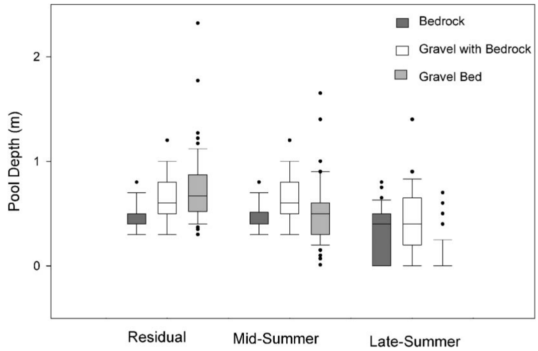

FIGURE 3.—Box-and-whisker plot of residual, midsummer (24 June–11 July), and late-summer (25–30 August) pool depths for three pool types in Harvey and Knowles creeks, Oregon, during 2002. The lower boundary of each box represents the 25th percentile, the midline represents the median, and the upper boundary represents the 75th percentile. The lower whisker represents the 10th percentile, the upper whisker represents the 90th percentile, and circles represent outlying points.

Results

Pool Size and Surface Water Availability

A total of 6.6 km of stream length was surveyed, which contained a total of 153 pools and 51 glides (Table 1). Residual pool depth (Figure 3) was significantly lower in bedrock pools than in the other pool types ($P = 0.0001$, one-way ANOVA). Median depth in each of the three pool types was less than 1 m. A few deep pools were measured in gravel-bed reaches (maximum depth = 2.3 m) and gravel pools with bedrock contact (maximum depth = 1.2 m); these depths were outside the range observed for bedrock pools (maximum depth = 0.8 m). Residual pool area (Figure 4) was slightly larger for gravel pools with bedrock contact than for other pool types ($P = 0.01$, one-way ANOVA).

Twenty-five percent of gravel-bed pools were already dry by midsummer, whereas no pools with bedrock contact were dry during this period (Figure 5). Pools with a bedrock control were more likely to persist throughout the summer dry season

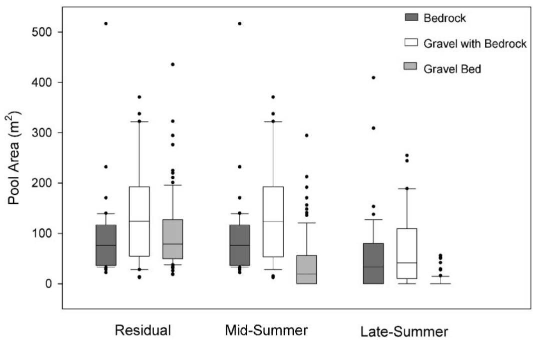

FIGURE 4.—Box-and-whisker plot of residual, midsummer (24 June–11 July), and late-summer (25–30 August) pool area for three pool types in Harvey and Knowles creeks, Oregon, during 2002. The lower boundary of each box represents the 25th percentile, the mid-line represents the median, and the upper boundary represents the 75th percentile. The lower whisker represents the 10th percentile, the upper whisker represents the 90th percentile, and circles represent outlying points.

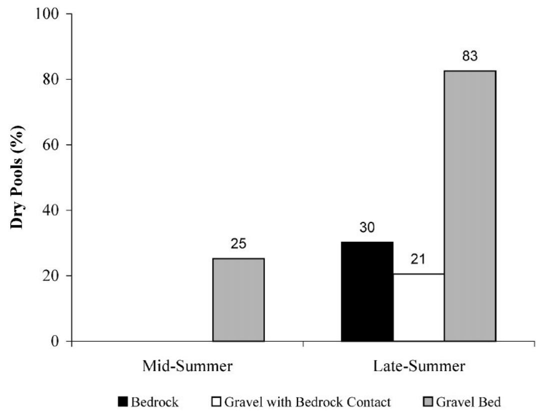

FIGURE 5.—Percentages of three pool types in Harvey and Knowles creeks, Oregon, that were dry by midsummer (24 June–11 July) and late summer (25–30 August) in 2002. Numeric values above the bars represent the actual percentages.

and exhibited the smallest individual decreases in pool depth and area. Seventy percent of bedrock pools remained wet by late summer, and the median decreases in pool depth and pool area were 17% and 40%, respectively. Seventy-nine percent of gravel pools with bedrock contact remained wet by late summer, and the median decreases in pool depth and area were 29% and 50%, respectively. Only 17% of gravel-bed pools persisted through late summer, accompanied by a 100% reduction in median residual pool depth and area.

Among pool types, deeper pools did not have a greater likelihood of remaining wet throughout the summer ($P = 0.05$, log-likelihood test in logistic regression). Within pool types, there was a positive correlation between residual pool depth and the likelihood of remaining wet throughout the summer for gravel-bed pools ($P = 0.02$, log-likelihood test in logistic regression).

Based on residual pool area, the greatest proportion of the total habitat area in both study basins consisted of gravel-bed pools. The majority of this habitat was unavailable, however, during late summer due to a lack of water (Figure 6). Bedrock pools had greater water availability and progressively became the dominant form of available habitat during the summer. By the end of the summer, connectivity was extremely limited for all pool types (Table 2), but the potential for invertebrate drift was highest in bedrock reaches due to the presence of continuous surface flow.

Depositional reaches (hereafter referred to as free-formed alluvial reaches) that plotted below an empirically derived threshold of drainage area and channel slope (Montgomery et al. 1996), recent debris-flow deposits, longitudinal distance from the mouth to the headwaters, and river basin were explanatory variables used to predict the occurrence of dry pools. Debris-flow deposits (a) and free-formed alluvial reaches (b) were highly significant variables ($P = 0.0001$, log-likelihood test) in a logistic regression model ($y = -0.73 + 2.50a + 3.02b$) that correctly predicted the occurrence of 70% of all dry units. No consistent longitudinal pattern ($P = 0.20$, log-likelihood test) or basin effect was detected ($P = 0.06$, log-likelihood test). Pools in free-formed alluvial reaches were 21

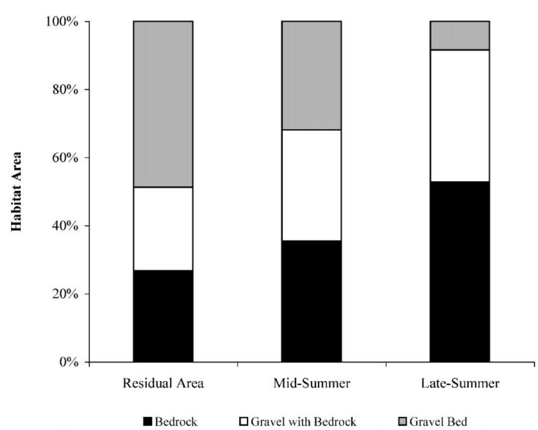

FIGURE 6.—Percentages of available residual, midsummer (24 June–11 July), and late-summer (25–30 August) pool habitat composed of three pool types in Harvey and Knowles creeks, Oregon, 2002.

TABLE 3.—Juvenile salmon abundance and density (SDs in parentheses) in three pool types during midsummer (24 June–11 July) and late summer (25–30 August) of 2002 in Harvey and Knowles creeks, Oregon. Fish densities were calculated based on wetted area.

Pool type	Total number of fish observed midsummer	Residual area median fish density (fish/m^2)	Midsummer median fish density (fish/m^2)	Total number of fish observed in late summer	Late-summer median fish density (fish/m^2)
Bedrock dominated	4,890	0.80 (0.95)	0.80 (0.73)	2,550	0.97 (0.85)
Gravel with bedrock contact	4,050	0.70 (1.20)	0.76 (1.11)	2,260	1.06 (0.91)
Gravel bed	5,110	0.75 (0.65)	1.02 (1.00)	880	1.39 (0.87)

times more likely to go dry than other stream reaches (odds ratio, logistic regression), and pools in debris-flow deposits were 12 times more likely to go dry (odds ratio, logistic regression). In addition to predicting areas susceptible to pool drying, free-formed alluvial reaches and debris-flow deposits correctly predicted the occurrence of 67% of gravel-bed pools in the study streams.

Changes in Fish Abundance

Divers observed a total of 14,050 salmonids (82% juvenile coho salmon, 18% trout) during the midsummer survey. Juvenile coho salmon were evenly distributed during the midsummer sampling period (present in 99% of pools and glides). Trout were less abundant and had a patchy distribution (present in 67% of pools and glides).

Due to the high variability in fish density among pool types (Table 3), no significant differences were detected during either time period ($P = 0.3$ based on midsummer wetted area, $P = 0.4$ based on late-summer wetted area, one-way ANOVA). Fish density remained relatively constant in bedrock pools throughout the summer. Pools in aggraded reaches progressively shrank throughout the summer, resulting in a 46% increase in fish density. This increase in density resulted in substantial crowding of fish in remnant pools. The seasonal increase in fish density was significantly higher in gravel-bed pools and gravel pools with bedrock contact than in bedrock pools (assessed as the change in density between midsummer and late summer within pool types, $P = 0.014$, one-way ANOVA).

Fish abundance decreased substantially in all pool types by late summer (Figure 7); however, the only statistically significant difference was detected for gravel-bed pools ($P = 0.0001$, one-way ANOVA). The decrease in fish abundance, presumably due solely to the desiccation of fish in dry pools, was 36% of the initial population. Mortality of fish desiccated in gravel-bed pools was a minimum estimate, because 25% of pools were already dry during the initial sampling period. Total fish abundance in the study areas decreased by 59% by late summer.

Stream Temperature

The partitioning of surface and subsurface flow in aggraded and bedrock reaches suggests that stream temperature could vary substantially among the different pool types. Our direct investigation was extremely limited, but in the three pools monitored, strong differences in stream temperature were observed (Figure 8). Diurnal temperature patterns fluctuated most in a bedrock pool that received surface flow from a shallow bedrock riffle upstream. In contrast, a bedrock pool that received no surface flow from upstream but that was recharged by subsurface flow discharging from fractured bedrock had relatively low water temperatures and almost no diurnal fluctuation. A gravel pool with bedrock contact that received a mixture of surface flow and hyporheic flow from an upstream riffle containing a thin veneer of alluvium over bedrock was intermediate between the two extremes. The observed temperature patterns should be considered a localized effect and not the result of longitudinal variation within the 1-km section of stream that the pools were located in. This is evident because the pool with the highest water temperature was situated upstream of the pools with lower temperatures. Additionally, there were no significant tributary inputs between the pools that were monitored for temperature.

Discussion

In Mediterranean climates, the summer dry season can be an extremely stressful period for aquatic organisms because of the scarcity of water and potentially high water temperatures. Although the occurrence of a summer drought is very predictable, its magnitude and extent are highly variable. Because the severity of the 2002 dry season was typical for low-flow conditions in the study area, our results have important implications for fish habitat, and inferences drawn from this study are not limited to extremely dry years.

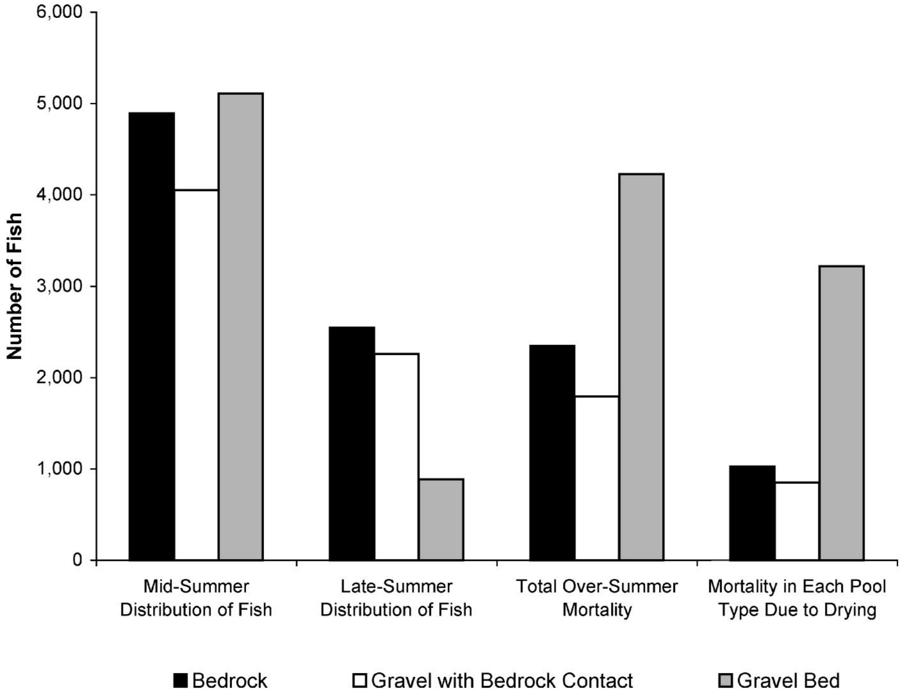

FIGURE 7.—Salmonid abundance in midsummer (24 June–11 July) and late summer (25–30 August), total summer mortality, and desiccation mortality within three pool types in Harvey and Knowles creeks, Oregon, 2002.

Available habitat for salmonids rearing during the summer dry season was strongly correlated with in-channel sediment storage. Residual pool depth was greatest in aggraded reaches; however, the lack of water made the majority of these deep pools unavailable during the summer, and substantial fish mortality occurred when streamflow in gravel-bed pools shifted to subsurface flow. Water was present in these channels for the duration of the summer, but was unavailable at the surface because it passed underneath the streambed as hyporheic flow. In contrast, pools with a bedrock contact had a greater likelihood of remaining wet than pools in aggraded reaches. Small, remnant pools persisted in aggraded reaches when pools were deep enough to contact subsurface flow or when sediment depth was relatively thin, allowing pools to scour to the underlying bedrock. Field evidence suggested that the size of remnant pools was proportional to the area of exposed bedrock at the pool bottom.

A common expectation in coastal regions of the Pacific Northwest is that winter rearing habitat constitutes the primary limiting factor for juvenile coho salmon production (Tschaplinski and Hartman 1983; Nickelson et al. 1992). Results of this study indicate that the summer dry season can also be a period of extremely high mortality in the life cycle of coho salmon and that water availability is one of the primary limitations for survival. Total fish abundance by late summer was 59% lower than midsummer abundance estimates, suggesting that the summer season can be a period of very high mortality. Although estimates of fish abundance based on snorkel surveys can lack the precision of other sampling methods (Hankin and Reeves 1988; Hillman et al. 1992), the magnitude of the difference suggests meaningful biological differences.

To interpret the effects of pool drying on fish survival, we must evaluate several alternative explanations for the change in fish abundance. Indirect effects of pool drying on fish survival include severe crowding and the loss of habitat area, which could cause high levels of physiological stress and/or increased risk of predation. As a direct effect, pool drying could result in acute mortality of fish due to desiccation. However, we cannot rule out the possibility that fish can burrow into the underlying substrate and seek refuge in the hyporheic zone. The effectiveness of the hyporheic zone as a refuge from drying is highly uncertain (Edwards 1998), and this alternative explanation seems unlikely because pools were dry

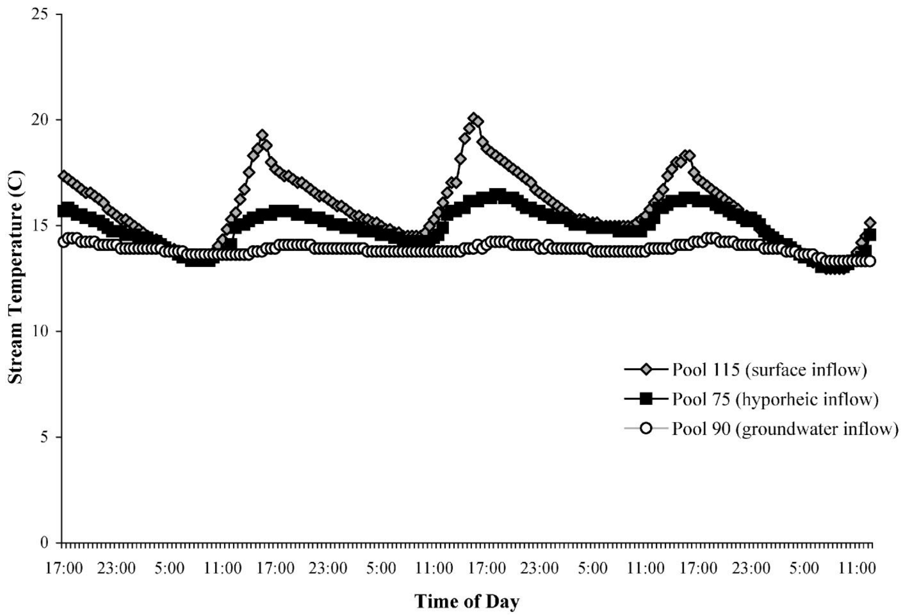

FIGURE 8.—Fluctuations in stream temperature for pools with different substrate and streamflow conditions within a 1-km reach of Harvey Creek, Oregon, during 26–30 August 2002. Pool 115 (bedrock-dominated) was located at the upstream end of the study reach and received surface flow from a shallow bedrock riffle. Pool 90 (a gravel pool with bedrock contact) was located 515 m downstream of pool 115 and received subsurface flow that emerged from fractured bedrock. Pool 75 (a gravel pool with bedrock contact) was located 735 m downstream of pool 115 and received a mixture of surface and subsurface flow from a riffle with a thin veneer of gravel over the underlying bedrock.

for an extended time period (weeks to months). Connectivity between pools was also very limited, so movement of fish to areas that had persistent surface water throughout the summer was also unlikely. Fish abundance did not increase between midsummer and late summer in any of the pools we observed, which suggests that movement was severely limited and that fish were not able to congregate in persistent pools.

The fraction of the initial population of salmonids that were lost to desiccation in dry pools by late summer was proportional to the fraction of bedrock pools and gravel pools with bedrock contact that went dry, suggesting that fish were evenly distributed among these pool types. In contrast, the proportion of gravel-bed pools that went dry (83%) was greater than the proportion of fish desiccation mortalities (63%). Midsummer fish density in gravel-bed pools that persisted throughout the summer was 43% higher (1.09 fish/m^2 residual area) than in gravel-bed pools that eventually went dry (0.62 fish/m^2 residual area). Within the gravel-bed pool type, deeper pools had a greater likelihood of remaining wet throughout the summer, and fish may have preferentially utilized these pools. Similarly, Labbe and Fausch (2000) observed that deeper pools had a higher probability of persisting through the summer dry season in an intermittent stream underlain by thick alluvial deposits. However, it is important to note that shallower bedrock pools had a greater overall likelihood of remaining wet throughout the summer than the deeper gravel-bed pools.

Field observations suggest that three factors influenced water availability in pools: (1) gravel depth, (2) bedrock topography, and (3) subsurface flow paths through fractured bedrock. Gravel depth influenced surface water availability by increasing the proportion of the low-flow stream water that traveled through the hyporheic zone. The relatively small size of pools in the study area suggests that scour was inadequate to create pool contact with the underlying bedrock in alluvial deposits greater than 1 m deep. The uneven surfaces of the underlying bedrock also compounded the problem of predicting water availability. When bedrock was exposed at the bottom of a pool, we could not determine whether the bedrock contact was (1) a slightly elevated ledge within the bank-full channel or (2) a trough where the low-flow stream water collected. Presumably, this could explain why some of the gravel pools with bedrock contact went dry. In addition, a few bedrock-dominated stream reaches also had intermittent surface flow. Impervious sandstone layers typically formed the channel bed, but the sandstone layers were interbedded with more erosive, more porous siltstone layers. Sandstone layers commonly had large fractures that allowed all or a portion of the streamflow to travel beneath the bedrock surface. Bedrock pools are typically formed by plucking, a process whereby fractures produce loosened blocks that are entrained and transported (Whipple et al. 2000). Plucking of large blocks exposed the porous siltstone layers, and subsurface flow was observed emerging from bedrock ledges. Infiltrating and emerging flow paths through the fractured bedrock have also been observed during studies of hillslope hydrology in this area (Anderson et al. 1997).

In some regions, broad valley floors that contain thick alluvial and glacial deposits function as recharge areas for the hyporheic zone (Stanford and Ward 1993). In upwelling zones, hyporheic exchange has the potential to greatly enhance summer habitat. However, this broad-scale pattern has not been observed in the Oregon Coast Range, where mountain streams are typically constrained within narrow valleys and where the hyporheic zone appears to be limited to the aggraded zone of the bank-full channel.

Predicting Areas Susceptible to Channel Aggradation and Pool Drying

This study established a direct linkage between physical channel structure and ecologically significant habitat characteristics. Two areas subject to pervasive channel aggradation were: (1) stream reaches that fell below a drainage area and channel slope threshold (Montgomery et al. 1996), and (2) thick sediment accumulations stored behind massive log jams that were delivered by debris flows. Based on these predictions, juvenile fish survival during the summer dry season can be estimated or modeled over a broader area.

Montgomery et al. (1996) identified an inverse relationship between drainage area and channel slope that separates bedrock reaches from free-formed alluvial reaches. The threshold is affected by the local influence of log jams, sediment supply, and clast lithology (Montgomery et al. 1996; Massong and Montgomery 2000). Alluvial reaches consistently plot at a lower average slope for a given drainage area, and are therefore expected to exhibit predictable and persistent alluvial bed morphology. Alluvial reaches are inherently depositional and are susceptible to pervasive, long-term channel aggradation. In contrast, stream reaches that plot above the threshold are limited to localized sediment accumulations stored behind log jams, boulder accumulations, and debris-flow deposits (Montgomery et al. 2003). Specific sites of aggradation in these areas are therefore transient and less predictable.

Similar to free-formed alluvial reaches, debris-flow deposits also had a high likelihood of going dry. These results indicate that temporal dynamics of sediment and wood supply, in addition to spatially explicit models based on slope–area relationships, are important considerations for predicting channel aggradation. In the Oregon Coast Range, landslides and debris flows can deliver large volumes of coarse sediment to river channels. These mass wasting processes can form extensive accumulations of wood that completely dam the channel and valley floor; the associated sediment deposits can be several meters thick and can inundate hundreds of meters of stream channel (May 2001, 2002). The architecture of these deposits is unique in small, coastal streams that lack the capacity to transport large volumes of wood by fluvial processes, because wood is typically large relative to channel size (Bilby and Ward 1989). Wood delivered from riparian forests adjacent to the channel typically create in-stream wood structures that consist of individual pieces or small accumulations. Alluvial deposits stored behind wood accumulations are typically thin because the depth of sediment is limited by the height of the wood accumulation; therefore, substantial channel aggradation is not possible in such areas. Debris-flow deposits may assume a greater relative importance in log-jam formation for streams bordered by industrial forests because of decreases in the size of wood recruited from the local riparian area (Montgomery et al. 2003) and increases in debris-flow frequency and magnitude associated with timber harvest and roads (May 2002).

A logistic regression model that included the location of free-formed alluvial reaches and recent debris-flow deposits accurately predicted the presence of 70% of dry pools at the reach scale, and identified the spatial occurrence of 67% of gravel-bed pools. Contrary to a common expectation that the likelihood of pool persistence throughout the summer would increase in a downstream direction due to increased drainage area, no consistent longitudinal pattern in water availability was detected by the logistic regression model. Patterns of pool drying were also similar between the two study basins.

Discontinuous Flow Patterns and Fish Energetics

Habitat connectivity is an important consideration for fish because it influences movement and the availability of food resources supplied from upstream sources. Pools that lack connectivity may provide only limited opportunities for growth because of the lack of invertebrate drift from upstream. Previous research in the Napa River, California, found that discontinuous flow patterns of dry riffles alternating with wet pools, as well as high water temperatures, resulted in low to negative growth of juvenile steelhead (Stillwater Sciences 2002). In three western Washington streams with a high degree of connectivity, juvenile coho salmon moved out of smaller and shallower habitat units, and fish that moved among habitat units grew faster than fish that remained in the same habitat unit (Kahler et al. 2001). These results indicate that small-scale, habitat- and growth-related movements are important components of summer rearing.

Limited sampling of stream temperature suggests that surface and subsurface flow paths substantially influence stream temperature at very fine spatial scales. The diversity of flow paths creates thermal heterogeneity, allowing fish inhabiting individual pools to experience different environmental conditions. High water temperatures can increase metabolic rates (Brett 1971) and therefore have a direct effect on growth. Based on the differences in temperature and connectivity among the different pool types we investigated, there may be a strong potential for differential growth among the pool types. Bedrock reaches appeared to have a greater supply of food because a higher proportion of riffles remained wet and had the potential to deliver invertebrate drift, whereas isolated pools were limited to in situ production and localized terrestrial inputs. The net effect of potentially greater food availability and increased fish metabolic costs (due to higher water temperatures) in bedrock reaches could not be determined in this study but is an important consideration for future research.

Patterns of seasonal growth and survival of salmonids in the Pacific Northwest are highly uncertain. Previous research has documented a positive correlation between summer streamflow and survival of juvenile coho salmon (Mathews and Olson 1980); however, no underlying mechanisms have been investigated. Summer growth of juvenile salmonids may be critical to population viability because larger fish generally have higher overwinter survival rates than do smaller individuals (Quinn and Peterson 1996). Larger smolts also have a greater likelihood of surviving the ocean phase of their life history (Yamamoto et al. 1999; Zabel and Williams 2002). In the Pacific Northwest, winter growth is often restricted by cold water temperatures, reduced primary production, and the need for juvenile fish to seek cover from high stream velocities (Bilby and Bisson 1992). In coastal streams of northern California, extremely low growth rates of juvenile coho salmon have been observed during the winter, followed by substantial increases in growth during spring (Bell 2001). If food or foraging opportunities are limited in the summer and winter, salmonid fishes may be highly dependent on growth accrued during spring and autumn for achieving a larger body size.

Summary and Implications for Land Management

Field investigations of channel aggradation and water availability during the middle of the summer dry season indicated that areas of high sediment storage were associated with slightly deeper pools. Late-summer surveys revealed that the majority of gravel-bed pools went dry because the streambed was extremely porous and allowed streamflow to drop below the bed elevation. Aggradation caused surface flow to become intermittent, which stranded fish in drying channels. In areas of low sediment storage, pool depth was limited by the underlying bedrock, but these pools were sustained by hyporheic flow and were more likely to persist throughout the summer dry season. These results illuminate an important temporal dynamic that occurs during the summer dry season, and serve as a reminder that field measurements taken at a single point in time can be a misleading indication of habitat quality when habitat conditions are spatially and temporally dynamic (Van Horne 1983).

Our results also address an important question about the influence of large influxes of sediment and wood on aquatic habitat, a subject that is currently undergoing a great deal of speculation. Because channel aggradation was directly linked to water availability and fish survival, this study demonstrates that increases in coarse sediment supply can be associated with sharp reductions in salmonid habitat and productivity. Land-use practices, such as timber harvest and road construction, are often associated with large influxes of coarse sediment in forested mountain streams, particularly through increases in landslide and debris-flow activity (Swanson and Dyrness 1975; Swanson et al. 1982; Madej and Ozaki 1996; May 2002). Similarly, severe wildfires, which are a major component of the disturbance regime in the Oregon Coast Range (Long et al. 1998), can also result in an accelerated rate of coarse sediment input (Swanson 1981; Meyer et al. 2001; May and Gresswell 2003). However, river systems are dynamic, and disturbance events that result in a short-term loss of habitat may be required to create productive habitat conditions over the long term (Reeves et al. 1995; Labbe and Fausch 2000). Aggraded channels may create important habitat for other life history stages during other seasons. For example, aggraded reaches can create spawning areas in channels that otherwise may be too coarse (Buffington and Montgomery 1999).

Reeves et al. (1995) hypothesized that the most complex habitat conditions and fish assemblages would form in watersheds that are at intermediate stages of disturbance and reorganization. Channels that are interposed between gravel rich and gravel poor may provide optimal habitat conditions, because deep pools can form in the stored alluvium and contact with the underlying bedrock provides consistent water availability and lower water temperatures. However, the biotic interactions caused by increased crowding of fish trapped in isolated pools and the lower food availability associated with discontinuous surface flow may offset the favorable abiotic conditions. Tradeoffs between short- and long-term effects of disturbance remain uncertain, but mountain streams that are susceptible to catastrophic disturbances like fires and debris flows will produce a dynamic condition in which not all habitats are suitable for salmonid production at a specific point in time.

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