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[Article]

The Response of Salmon Populations to Geomorphic Measurements at Three Scales

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Abstract.—Protocols to assess stream channel response to disturbances often focus on physical aspects of the stream at the reach scale without measurements of fish populations. In this study, estimates of juvenile salmon abundance in 511 habitat units within 25 reaches of 12 streams were made over 4 years and juxtaposed with measurements of physical habitat at the habitat unit, reach, and watershed scales. Fish ranged in size from about 50 to 160 mm fork length. The amount of variation among densities differed by species and geographic scale. For most species, the habitat unit scale accounted for the most variation. Relationships between salmon density and measurements at the habitat unit scale varied. At the reach scale, we observed a negative relationship between abundance of coho salmon *Oncorhynchus kisutch* parr and number of pools. A positive relationship appeared between coho salmon parr and large wood. At the watershed scale, a positive relationship was observed between coho salmon parr and valley morphology. Valley morphology also entered the model for cutthroat trout *O. clarkii*. Differences in salmonid densities observed between northern and southern watersheds were attributed to differences in landforms, geology, and soils among islands in southeast Alaska. Simple habitat measures, such as pool counts, were not good predictors of fish abundance. However, geomorphic measures from multiple scales that are accompanied by estimates of fish abundance can provide managers with an integrated picture of watershed productivity and a better means to evaluate features that influence productivity.

Protocols used to assess stream channel condition often focus on measurements of physical habitat at one geographic scale and usually do not include measurements of fish abundance (Johnson et al. 2001; Stolnack et al. 2005). Salmonid abundance is influenced by complex biological and physical factors at multiple geographic scales (Meehan 1991; Nickelson et al. 1992; Minns et al. 1996; Rosenfeld et al. 2000; among others). The number of fish in a pool may be related to the presence of large wood; however, geographic features at the watershed scale that affect such things as upstream spawning area or off-channel habitat also can have an important influence on fish abundance in the pool (Reeves et al. 1989; Shuter 1990; Dunning et al. 1992; Nass et al. 1996; Pess et al. 2002; Benda and Sias 2003). In southeast Alaska, watersheds located in karst landscapes tend to support more freshwater-rearing coho salmon *Oncorhynchus kisutch* than nearby watersheds (Murphy et al. 1986; Bryant et al. 1998).

An implicit assumption in many protocols used to assess stream habitat is that changes observed in the physical measurements will be accompanied by corresponding changes in the abundance of salmon. Most of the physical variables (e.g., large wood and pools) used in monitoring protocols are derived from studies that have established a statistical or inductive relationships with fish abundance. For example, large wood and pools (Bisson et al. 1987; Fausch and Northcote 1992; Harvey 1998; Solazzi et al. 2000; Roni and Quinn 2001), bankfull width, cover, undercut banks, depth, and velocity (McMahon 1983; Heifetz et al. 1986; Marcus et al. 1990; Nickelson et al. 1992; Nass et al. 1996; Rosenfeld et al. 2000; Sharma and Hilborn 2001) have been shown to affect salmon abundance and production. Sharma and Hilborn (2001) used production per kilometer of stream and found positive relationships with pool, pond, and large woody debris (LWD) density and negative relationships with stream gradient and valley slope. Bradford et al. (1997) found that smolt abundance was not a particularly good predictor of habitat quality. Pess et al. (2002) observed a decrease in salmonid abundance with large-scale effects such as agriculture and urbanization. Some of these studies focused on watershed-scale effects, but most were oriented toward the response of salmonid

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TABLE 1.—The southeast Alaska streams and number of reaches and habitat units where fish population were estimated and habitat was measured each year during 1997 through 2000.

Stream	Year sampled	Number of reaches	Number of habitat units
Painted Creek	1997	3	49
	1998	2	52
	2000	2	48
Sal Creek	1997	1	32
Trap Creek	1997	3	59
Fowler Creek	1998	2	47
Maybeso Creek	1998	2	60
South Fork Staney Creek	1998	1	26
Kadake Creek	1999	1	20
Kadashan River	1999	3	45
Cable Creek	2000	1	22
Duckbill Creek	2000	1	9
Pile Driver Creek	2000	2	29
Snipe Creek	2000	1	13

populations to instream effects and do not incorporate multiple geographic scales.

We incorporated estimates of salmon abundance (measured by density) into a protocol used to assess stream channel condition at the reach scale (Woodsmith et al. 2005) and extended the analysis to the response of salmonid density to physical habitat at three hierarchical scales: habitat unit, reach, and watershed. We examined relationships between salmon abundance and separate physical habitat measures at each scale. Our goal was to examine the effect of geographic scale on measurement of salmon abundance and to determine which habitat characteristics influence salmon abundance at different scales.

Methods

Study sites.—Study watersheds were located in the temperate rainforest of southeast Alaska (Harris et al. 1974). They were a subset of watersheds sampled to develop a channel-condition assessment protocol to monitor land management effects on stream channels (Bryant et al. 2005; Woodsmith et al. 2005). We sampled 12 streams selected from a larger group surveyed by Woodsmith et al. (2005; Table 1; Figure 1). The geographic distribution range of the streams extends more than 450 km north to south along the southeast Alaska archipelago.

The three geographic scales were habitat unit (mean area = 283 m^2), reach (mean area = 5,161 m^2), and watershed (mean area = 17.5 km^2). A habitat unit was defined by three criteria: a unique hydrologic control, a minimum residual depth (RD), and a length or width greater than 0.10 times the average channel bed width for the reach (USDA Forest Service 2001). Habitat units were located within a reach and were separated from each other by an easily identifiable hydrological control (i.e., log, gravel bar, riffle, etc.). They commonly included more than one geomorphic pool, as defined by Woodsmith et al. (2005). Reach units were approximately 20 channel lengths long. All of the reaches were alluvial, single-thread (i.e., not braided and without significant side channels), gravel-bedded flood plain channels with gradients less than 0.025 (Woodsmith et al. 2005). Watersheds included the drainage area above the lowest reach that was sampled and were estimated from data in the Tongass National Forest geographical information systems (GIS) database.

Sample methods.—The study reaches began at a randomly selected distance of 1–10 channel widths from where the stream was accessed, such as a road crossing or trail. The start and end points of each reach were selected so that each end had a shallow, fast-water riffle, a fully spanning log dam, or other distinct hydrologic control. After each reach was defined, smaller habitat units were identified within each reach. All habitat units were counted and identified. Fish populations were sampled in at least 50% of randomly selected habitat units in the reach. Each unit was separated from adjacent units by a hydrologic control. The control was a structure, such as a shallow riffle or fully spanning instream log, that would prevent or inhibit short-term (<6 h) movement of fish between habitat units.

The study was conducted over 4 years from 1997 through 2000. Painted Creek was sampled in all years except 1999. Three reaches in Painted Creek were sampled in 1997. We dropped one reach and the remaining two reaches were sampled in 1998 and 2000. In all other streams, each reach was sampled in 1 year. All sampling was conducted during the summer, late June through early September. Habitat surveys were completed a few days after fish populations were sampled.

Fish were captured with minnow traps that were baited with salmon eggs held in perforated Whirl-paks (Bloom 1976; Bryant 2000). Traps were set on the stream bottom parallel to the flow next to suspected salmonid rearing habitats, such as debris accumulations, rootwads, or undercut banks. Traps were distributed to completely sample the habitat unit and to maximize the number of fish captured. Distance between traps depended on habitat complexity, but generally traps were separated by about 2 m. Riffles were not directly sampled by the minnow traps because riffles were too shallow, but traps were set adjacent to them. Population estimates were made in each habitat unit with a removal method using three to preferably four capture occasions (Bryant 2000). Between 40 and

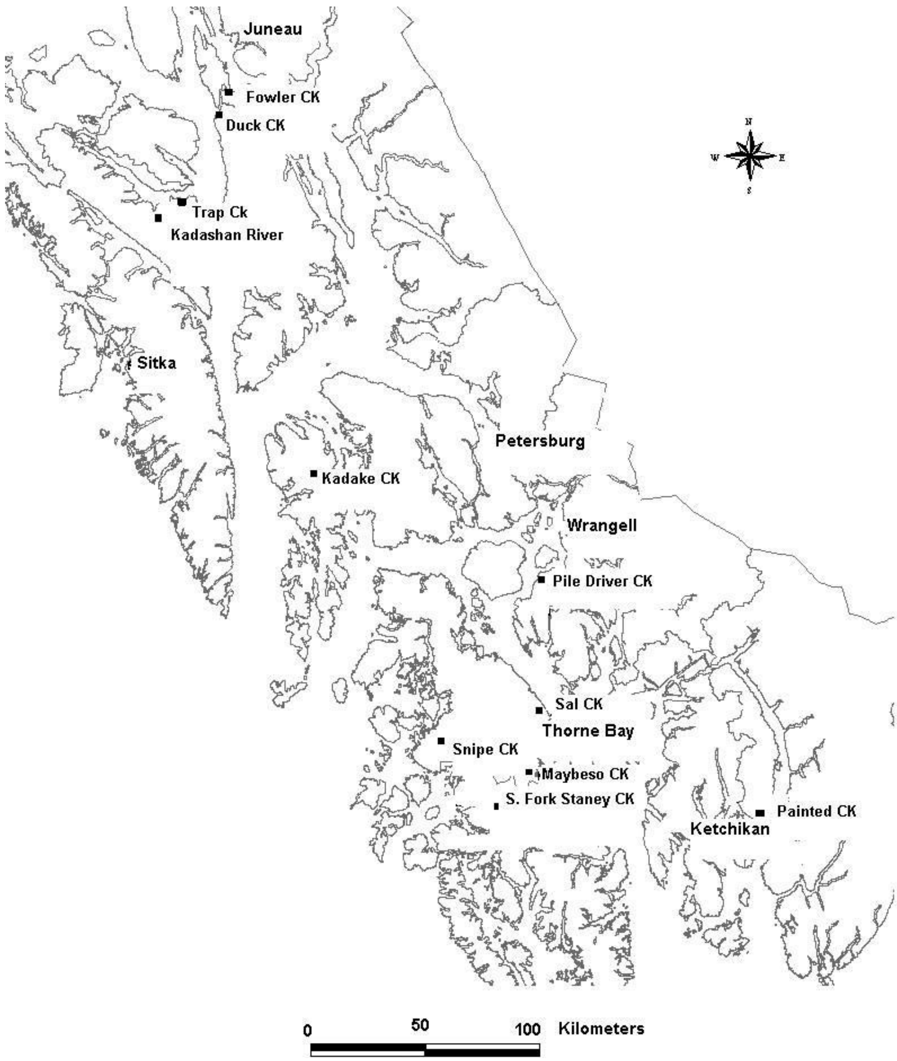

FIGURE 1.—The location of southeast Alaska watersheds (dots; CK = creek) sampled for salmonid population and habitat evaluations, 1997–2000. Primary towns (boxes) are included for reference.

50 traps were set for each removal experiment. Usually two or more habitat units were sampled concurrently. Traps were left undisturbed for 80–100 min. After 90 min, they were picked up in the same order in which they were set. Fish were removed and fresh bait was placed in the trap. Each trap was set again in the same location. Fish from each habitat unit and capture occasion were segregated and processed separately. While the second set was fishing, fish from the first set were identified, counted, and measured (fork length; mm). The procedure was repeated for each capture occasion. Fish from each capture occasion were placed in a holding pen (or blocked minnow traps). When the last capture occasion was completed, all fish were returned to the same area where they were captured. Population estimates were computed by species for each habitat unit. Coho salmon were separated into fry and parr by length frequency distribution. Coho salmon were considered to be fry if they were less than 50 mm in June, less than 55 mm in July, or less than 60 mm in August.

Population estimates were made for each habitat unit using Capture software program (White et al. 1982). If four capture occasions were used, population estimates were made, using the generalized removal estimate, with both equal probabilities of capture (P_c) among occasions and unequal P_c between the first and subsequent occasions. The program tests whether P_c

is constant based on a chi-square test ($\alpha = 0.05$). If the difference was significant, the estimate using unequal P_c was used; otherwise, the estimate using a constant P_c was used (see White et al. 1982). Four capture occasions are required to estimate populations with unequal P_c, and if only three capture occasions are completed, then a constant P_c is used (White et al. 1982).

Densities for each unit were computed by dividing the number of fish (sorted by species and size-group) by the area (m^2) of each habitat unit. The mean density for each reach was computed by dividing the sum of densities for species or size-groups by the number of units that were sampled in the reach. The mean density for each stream was the sum of the mean densities of each reach divided by the number of reaches in each stream.

Habitat measurements.—Measurements at the habitat unit scale were pool area (Parea), RD, total pieces of LWD (TLWD) per meter, and key pieces of LWD (KLWD) per meter; measures followed protocols used for stream surveys in southeast Alaska (USDA Forest Service 2001). The lengths and widths of all habitat units in the reach were measured and used to determine unit area. Residual depth was measured as the difference between the maximum depth and the depth of the hydrologic control at the lower end of the unit (Lisle 1987). The minimum residual pool depth was determined as follows: (average bed width in meters $\times$ 0.01) + 0.15 m. The minimum size used for LWD was 3 m long and 0.3 m wide. In streams where the average channel bed width was between 10 and 20 m, pieces of wood were counted as KLWD if they were 0.6 m in diameter, longer than 7.6 m, and lacked a rootwad (or had a rootwad with a diameter $>$3.0 m). For stream channels that were greater than 20 m wide, wood was counted as KLWD if it was longer than 15 m.

Variables used at the reach scale were designed to describe stream channel morphology and are described in Woodsmith et al. (2005). They included large wood per meter (TLWD), pools per meter (Poolspm), reach gradient (Slope), average RD (ARD), substrate size (AvgD50), and width-to-depth ratio (WD). Pool abundance and measures of large wood were standardized to reach length. Different variables were measured at the reach scale than were measured at the habitat unit scale. Pools were defined as topographic depressions in the streambed having (1) an RD equal to or greater than the threshold calculated as minimum RD = (0.02 $\times$ mean bed width in meters) + 0.05 m and (2) a length or width at least 10% of the mean bed width. This RD threshold was developed from southeast Alaskan data collected over a wide range in channel widths and is therefore appropriate for among-reach comparison. Large wood was a log or other piece having measures within the bankfull channel that were greater than 10 cm wide and 1 m long. Woodsmith et al. (2005) provide additional detailed descriptions of the variables, methods, and quality control criteria for the measurements.

Measures at the watershed scale, taken from GIS layers for the Tongass National Forest, were watershed area (Wsarea) and valley morphology (Valleywl). Valley morphology was represented by the ratio of watershed width (measured at the widest point) to watershed length.

Statistical analysis.—The relationships between fish density and habitat measures were explored separately for each geographic scale with a stepwise regression that used fish density by species and habitat measures at each scale. We considered the analyses to be exploratory and included variables in the stepwise regression at an α of 0.10 or less (SAS Institute 2001). Relationships among scales and habitat measures were not combined because the sample size (number of streams) was too small to combine all scales for analysis. At the habitat unit scale, independent variables were Parea, RD, TLWD, and KLWD. Density of Dolly Varden *Salvelinus malma* was included in the analysis for coho salmon fry and parr; coho salmon fry and parr were included in the analysis for Dolly Varden. Cutthroat trout *O. clarkii* and steelhead *O. mykiss* were not present in all streams, but in many streams they did occur together. They were not included in the analysis of other species. At the reach scale, independent variables were Poolspm, TLWD, ARD, WD, AvgD50, and Slope. The dependent variable was mean density of fish by species in each reach. At the watershed scale, independent variables included Wsarea and Valleywl. The mean density of fish by species in each of the 12 streams was the dependent variable. To avoid pseudoreplication in the watershed analysis, only 1 year, the most recently sampled year (2000), was used for Painted Creek.

The variance components of fish populations for habitat units, reaches, and watersheds were estimated using a nested analysis of variance model (SAS Institute 2001). It considered all streams with four variance components: among years, among streams within year, among reaches within year and stream, and among habitat units within year, stream, and reach. A separate analysis of the 3 years of repeated measures of reaches in Painted Creek used three variance components: among reaches, among years within reaches, and among pools at the habitat unit scale within years and reaches. The response variable was fish density of each species for both sets. Densities were transformed using

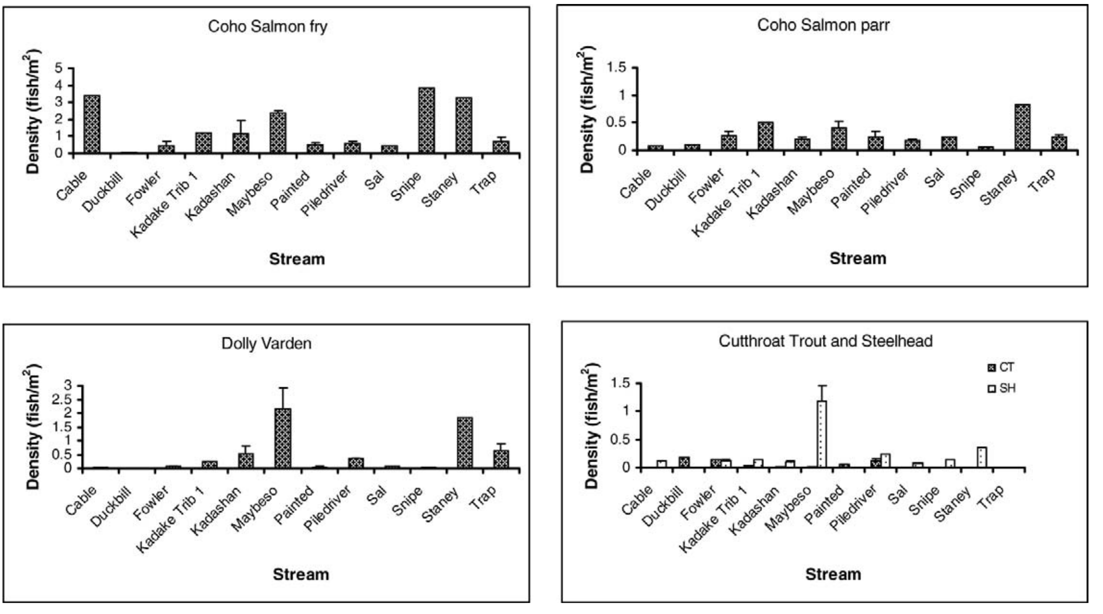

FIGURE 2.—Mean densities (+SE) of coho salmon fry and parr, Dolly Varden, cutthroat trout, and steelhead sampled in habitat units of 12 study streams throughout southeast Alaska, 1997–2000.

natural logarithms to reduce skewness to the right and create a near normal distribution.

Results

Salmonid Populations

Coho salmon were found in all streams and coho salmon fry were the most abundant; Dolly Varden were also common and were found in all streams except Duckbill Creek (Figure 2). Steelhead and cutthroat trout were present in some streams but were absent in others. Population estimates were reasonably precise as measured by probability of capture: 0.47 for coho salmon fry and 0.65 for cutthroat trout (Table 2). A wide range in densities among habitat units was observed for all species (Figure 3). Coho salmon fry ranged from less than 0.1 to 6.4 fish/m^2, and Dolly Varden ranged from less than 0.01 to 7.2 fish/m^2.

TABLE 2.—Means and ranges of probabilities of salmonid capture as used for population estimates in habitat units sampled in southeast Alaska during 1997 through 2000.

	Probability of capture	
Species	Mean	Range
Coho salmon		
Fry	0.47	0.255–0.999
Parr	0.59	0.250–1.000
Cutthroat trout	0.65	0.250–1.000
Dolly Varden	0.57	0.250–1.000
Steelhead	0.56	0.250–1.000

Density was highly skewed; a few habitat units supported high densities, but most supported considerably lower densities (Figure 3). A few streams tended to support higher densities of coho salmon fry and parr than most other streams (Figure 2). Considerably higher densities of steelhead parr were observed in Maybeso Creek than in other streams of the study.

The amount of variation among densities differed by species and geographic scale. In the analysis of all streams over multiple years, habitat unit (i.e., the

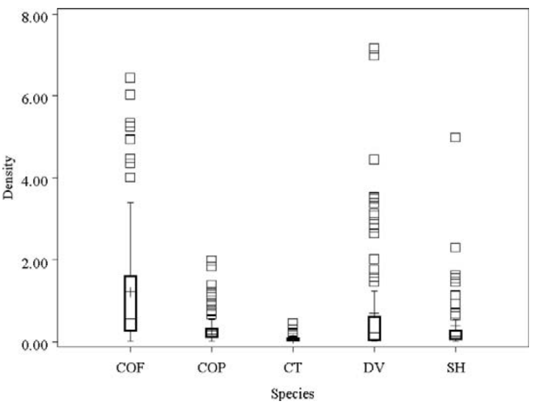

FIGURE 3.—Box plot of density estimates (fish/m^2) for coho salmon fry (COF) and parr (COP), cutthroat trout (CT), Dolly Varden (DV), and steelhead (SH) in all habitat units sampled in streams across southeast Alaska, 1997–2000.

TABLE 3.—Variation (%) observed among fish densities for all southeast Alaska streams, where variables include years in the study set and habitat unit, reach, and stream scales.

Source of variation	Coho salmon Fry	Coho salmon Parr	Cutthroat trout	Dolly Varden	Steelhead
Year	0.0	2.6	0.5	7.7	2.2
Stream	57.2	0.0	7.5	34.0	26.5
Reach	0.0	22.9	25.2	4.0	0.0
Habitat unit	42.8	74.6	66.8	54.3	71.3

TABLE 4.—Variation (%) observed among fish densities in southeast Alaska's Painted Creek, where variables include years in the study set and habitat unit and reach scales.

Source of variation	Coho salmon Fry	Coho salmon Parr	Cutthroat trout	Dolly Varden
Year	19.5	33.7	0.0	4.3
Reach	0.0	0.0	13.6	18.0
Habitat unit	80.5	66.3	86.4	77.6

smallest geographic scale) accounted for the most variation among fish densities, except for coho salmon fry, where it accounted for 43% (Table 3). Streams accounted for the largest component of variation for coho salmon fry but accounted for a negligible amount for coho salmon parr. Variation among years was relatively small for all species. Reach accounted for the second-greatest amount of variation for coho salmon parr and cutthroat trout.

Differences among years appeared in Painted Creek, where the same reaches were sampled during a 3-year period (Figure 4). Habitat unit accounted for the most variation for all species in Painted Creek (Table 4). Variation among years was small for cutthroat trout and Dolly Varden. Year accounted for 19.5% the variation for coho salmon fry and 33.7% for parr. The higher variation observed for coho salmon may be due to their anadromous life cycle; however, the analysis only includes 3 years.

Habitat Relationships

Few significant ($\alpha = 0.10$) relationships were observed between fish and habitat measures at the habitat unit scale (Table 5). Coho salmon fry were inversely related to Parea, indicating more fish in smaller pools. Coho salmon fry were positively related with the abundance of Dolly Varden. No habitat variable entered the model for coho salmon parr; however, a positive relation appeared with Dolly Varden. Residual depth entered the model ($\alpha = 0.10$) for steelhead; TLWD entered the model for cutthroat trout. However, relationships were weak and correlation coefficients were low for all relationships.

At the reach scale, four physical measurements—ARD, Poolspm, TLWD, and AvgD50—entered the stepwise regression models (Table 6). Coho salmon fry and parr and steelhead were positively related with Dolly Varden, and Dolly Varden were positively related with coho salmon parr (Table 6). Contrary to expectations, coho salmon parr were negatively related to Poolspm; however, they were positively related to large wood. For steelhead, the reverse appeared; they were positively related to Poolspm and negatively related to large wood. In all cases, the partial (and model) R^2 was low.

At the watershed scale, valley morphology entered the model for coho salmon parr and cutthroat trout (Table 7). The relationship was positive for coho salmon but was negative for cutthroat trout. Coho salmon may be more abundant in broad valleys and cutthroat trout more abundant in more constrained

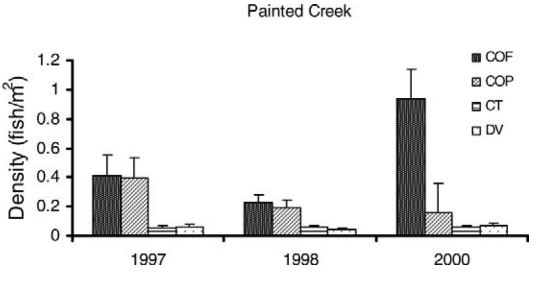

FIGURE 4.—Mean densities (+SE) for coho salmon fry (COF) and parr (COP), cutthroat trout (CT), and Dolly Varden (DV) sampled in habitat units of southeast Alaska's Painted Creek in 1997, 1998, and 2000.

TABLE 5.—Habitat unit-scale variables entering the stepwise regression model ($\alpha = 0.10$) for salmonid densities, by species, in southeast Alaska streams, where variables are coho salmon fry (COF), coho salmon parr (COP), Dolly Varden (DV), pool area (Parea), large woody debris (LWD), and residual depth (RD).

Variable	$P > F$	Regression parameter	Partial R^2
Coho fry salmon			
DV	<0.0001	0.510	0.290
Parea	0.066	−0.001	0.0324
Coho salmon parr			
DV	<0.0001	0.149	0.316
Dolly Varden			
COP	<0.0001	1.59	0.316
COF	0.0001	0.360	0.128
Cutthroat trout			
LWD	0.008	0.396	0.129
Steelhead			
RD	0.049	0.388	0.066

TABLE 6.—Reach-scale variables entering the stepwise regression model (α = 0.10) for salmonid densities, by species, in southeast Alaska streams, where variables are average residual depth (ARD), Dolly Varden (DV), total large woody debris per meter (TLWD), number of pools per meter (Poolspm), coho salmon parr (COP), substrate size (AvgD50). For cutthroat trout, no variable entered the model at $\alpha = 0.10$.

Variable	$P > F$	Regression parameter	Partial R^2
Coho fry salmon			
ARD	0.01	0.565	0.273
DV	0.050	4.123	0.128
Coho salmon parr			
DV	0.010	0.105	0.199
TLWD	0.010	0.476	0.276
Poolspm	0.070	−1.628	0.083
Dolly Varden			
COP	0.014	1.58	0.253
AvgD50	0.09	−14.27	0.105
Steelhead			
DV	<0.0001	0.576	0.79
TLWD	0.002	−0.980	0.121
Poolspm	0.080	3.31	0.028

TABLE 7.—Watershed scale variables entering the stepwise regression model ($\alpha = 0.10$) for salmonid densities, by species, in southeast Alaska, where variables are valley width-to-length ratio (Valleywl) and watershed area (Wsarea). For Coho salmon fry, no variable entered the model.

Variable	$P > F$	Regression parameter	Partial R^2
Coho salmon parr			
Valleywl	0.040	0.000001	0.36
Dolly Varden			
Wsarea	0.050	0.0006	0.41
Cutthroat trout			
Valleywl	0.004	−0.000001	0.84
Steelhead			
Wsarea	0.010	0.0003	0.62

valleys. A positive relationship with Wsarea was observed for Dolly Varden and steelhead (Table 7).

Differences in fish densities appeared between watersheds in southern versus northern areas of southeast Alaska. The mean density of coho salmon fry was 0.46 fish/m^2 (N = 4) in northern watersheds and 2.16 fish/m^2 ($N = 7$) in southern watersheds. This difference was significant ($P = 0.02$) in a two-sample t-test assuming unequal variances. Mean densities for coho salmon parr were 0.18 fish/m^2 (north) and 0.34 fish/m^2 (south), but differences were not significant ($P = 0.16$).

Discussion

The amount of variation in fish densities differed with geographic scale. The smallest spatial scale (habitat unit) accounted for the most variation in density for most species. Habitat units varied in size (10 to 1,650 m^2) and complexity. Most were composed of a several small pools that were interconnected. Variation at the reach scale was less than at the habitat unit scale. Reaches, by design, were relatively homogenous throughout the sampling regime (Woodsmith et al. 2005). All were floodplain channels with a low gradient and mostly gravel streambeds. Stratification at the reach scale undoubtedly reduced variation among density estimates at the reach scale. The reaches correspond to floodplain process groups (as defined by Paustian et al. 1992) and have been shown to be useful in stratifying stream reaches for salmonid abundance (Bryant et al. 1991). Although the streams were located in island watersheds of small or moderate size and share many common attributes (e.g., forest vegetation, climate, and features) associated with temperate rainforests (Harris et al. 1974), they varied in geology, geomorphology (Nowacki et al. 2001), and management status.

The physical measurements at the habitat unit scale were features that could be directly measured, so measurable criteria were used to define pieces of wood and pool depth. Although relationships appeared in the stepwise regression models between fish and physical measures, they accounted for only a small amount of variation in the models. Water velocity is often not included in stream habitat surveys and was not measured in our assessment because it is related to stream stage and would vary between sample periods. Nonetheless, water velocity can have an important influence on the distribution of fish (Mackinnon and Hoar 1953; Bovee 1986; Baltz et al. 1991; Aadland 1993; Piccolo et al. 2008). A deep scour pool with high flows relative to other locations in the reach is not as likely to support as many fish as a pool with lower water velocities.

The positive relationship between coho salmon parr and Dolly Varden suggests that both are responding to similar features, but the physical variables in the models for the two species were not consistent. However, the relationship supports the premise that good habitat for one is good for the other, and where there are more coho salmon parr it is likely that there will be more Dolly Varden, at least for streams at low gradients.

Precision of the habitat measurements at the reach scale was an overriding factor in variable selection (Woodsmith et al. 2005). The criteria used to identify pools for geomorphic purposes were well-defined and measurable; however, they did not capture criteria that are commonly associated with pool complexity, such as amount of cover, water velocity, shape, size, and location within the reach. These are difficult to measure consistently but are important for fish (McMahon 1983; Rosenfeld et al. 2000; Sharma and Hilborn 2001). Quality of a pool makes a difference to fish, and counts of pools, which are easy to measure, do not capture variation in pool habitat quality (Roni and Quinn 2001).

Large wood is one measure that contributes to pool complexity and can be measured quantitatively. Pools with large wood are likely to support more fish than a scour pool with little cover and fast water. However, in this study, measurements of large wood were not associated with pools when they were counted. Density of coho salmon parr was positively correlated with large wood, which is consistent with current paradigms (Bryant 1985; Beechie and Sibley 1997; Harvey 1998; Rosenfeld et al. 2000; Roni and Quinn 2001), but the correlation coefficient was low, indicating that other factors also influenced abundance.

Features that contribute to greater productivity at the landscape scale are not as well established as those at smaller scales for southeast Alaska. At the watershed scale, watershed shape appeared to influence fish abundance. Burnett et al. (2007) used a valley width index to identify the intrinsic habitat potential for coho salmon parr and steelhead in Oregon. The potential was higher for coho salmon parr in unconstrained valleys and higher for steelhead in more constrained valleys. They also reported higher intrinsic potential values for coho salmon in lower-gradient systems, whereas higher values for steelhead occurred in higher-gradient systems. The potential for both was low as the gradient approached 6%. Pess et al. (2002) implicated a positive relationship between landform and coho salmon abundance, finding higher abundances at lower-gradient watersheds. In the absence of brook trout *Salvelinus fontinalis*, Dunham et al. (1999) found geographic gradients associated with cutthroat trout; however, these were associated with thermal regimes. These and other studies reinforce the importance of landscape effects on salmonid populations (see Dunham and Rieman 1999; Thompson and Lee 2000).

The relationship that we observed indicates that coho salmon abundance will increase as watershed width increases relative to length. As a general observation for southeast Alaska, these watersheds tend have wider floodplains and more low-gradient tributaries than watersheds in steeper landscapes (R. Wissmar, R. Timm, and M. Bryant, unpublished manuscript). In southeast Alaska, small tributary and off-channel habitats are important for coho salmon parr, and these habitats would contribute to densities in the main-stem reaches that were sampled in this study (Bryant 1984; Gray and Marriott 1986; Bramblett et al. 2002; Schaberg 2006). Several landscape features on Prince of Wales Island (i.e., watersheds in lower-elevation terrain with moderate topography, distribution of karst throughout the island, and complex stream networks) may contribute to higher densities of coho salmon parr that were observed in the southern watersheds of the study (Wissmar et al. 1997; Bryant et al. 1998; Nowacki et al. 2001). As the GIS database for southeast Alaska matures with greater resolution of digital elevation models and of other data layers, more precise models of watershed productivity can evolve.

Measurements of the physical habitat of streams and watersheds are important to assess the ability of a watershed to support salmonid populations. Important criteria for the selected variables are that they be measurable (i.e., objective), reasonably precise, and repeatable (Woodsmith and Buffington 1996; Roper et al. 2002; Archer et al. 2004; Woodsmith et al. 2005). It is equally important that they capture features that affect fish abundance. Geomorphic measures that are precise and repeatable can detect relatively small changes in the physical conditions in stream reaches, but the response of salmon populations to small or moderate changes may not be detectable. Furthermore, the effects of small or moderate changes may be masked by interacting factors such as cover (i.e., large wood) and water velocity or other covariates at different scales. The response of coho salmon parr to the loss of a few (e.g., 10%) of geomorphic pools will depend upon the quality of the pools and what replaces them. If, for example, small, open scour pools are replaced by a larger pool with large wood (or, even better, a rootwad) that reduces water velocity, then the number of fish in the pool is likely to increase. Inclusion of complexity in habitat measures can improve their relevance to fish populations. One solution is to stratify pools into those with large wood and those without wood or into fast-water pools and slow-water pools, assuming that some suitable criteria for large wood and fast versus slow are established.

Relationships among fish density and an array of variables, including species interactions, were observed at all geographic scales (Table 8). However, most had low coefficients of variation, which suggests that more complex relationships exist than were detected. Relatively simple and easy-to-measure habitat features at the habitat unit and reach scales may not be good predictors of fish abundance. Interactions among different geographic scales may be important, but large sample sizes are necessary (Imhof et al. 1996) to quantitatively evaluate these. Even in the absence of large sample sizes, often prohibitively expensive, watershed-scale features can contribute to the predic-

TABLE 8.—Variables entering the stepwise regression models for each salmonid species (at α = 0.05** or α = 0.10*) for each geographic scale in southeast Alaska (COF = coho salmon fry, COP = coho salmon parr, DV = Dolly Varden, ARD = average residual depth, Parea = pool area, TLWD = total large woody debris per meter, Valleywl = valley width-to-length ratio, Poolspm = number of pools per meter, AvgD50 = substrate size, and Wsarea = watershed area).

Habitat unit scale	Reach scale	Stream scale
	Coho salmon fry	
DV**	ARD**	None[a]
	DV**	
Parea*		
	Coho salmon parr	
DV**	DV**	Valleywl**
	TLWD**	
	Poolspm*	
	Dolly Varden	
COF**	COP**	Wsarea**
COP**	AvgD50*	
	Cutthroat trout	
TLWD**	None[a]	Valleywl**
	Steelhead	
RD**	DV**	Wsarea**
	TLWD**	
	Poolspm*	

[a] No variable entered the model.

tive power of observations at smaller scales. We identified three features that appear to influence salmonid density, including valley shape, watershed size, and latitude. In this instance, watershed morphology (Valleywl) influenced number and species distribution: more steelhead in constrained valleys and more coho salmon in unconstrained valleys. These can be useful when evaluating relationships between fish and the physical habitat at smaller scales and in the design of fish and habitat monitoring programs. As relationships at multiple levels are identified, they may be included as covariates in models used to monitor management activities (Bryant et al. 2008).

Inclusion of fish population estimates in stream channel assessments can greatly enhance their utility to land managers. Most habitat assessments lack adequate models to relate differences in habitat to fish numbers (Stolnack et al. 2005). Population estimates made concurrently with habitat measurements will allow managers to evaluate the range of habitat conditions and changes in habitat condition in terms of fish numbers. Monitoring protocols that include multiple geographic and temporal scales are essential to determine watershed condition, assess management activities, and evaluate effects of natural and anthropogenic disturbances. Estimates of fish numbers (relative abundance, density, etc.) are the currency to evaluate habitat monitoring protocols.

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