

The Relationship between Productivities of Salmonids and Forest Stands
in Northern California Streams

by

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ABSTRACT

Productivities of resident salmonid populations, upland, and riparian areas in 25 small watersheds of coastal northern California were estimated and compared. The intention was to determine if: 1) upland site productivity predicts riparian site productivity; 2) either upland or riparian site productivity predicts salmonid productivity; and 3) other parameters explain more of the variance in salmonid productivity than upland or riparian site productivity. Salmonid productivity was estimated based on total salmonid biomass, length of age 1 fish, and percentage habitat saturation. Upland and riparian site productivities were estimated using site indices (tree height at 50 yr of dominant and co-dominant individuals) for redwood Sequoia sempervirens and red alder Alnus rubra, respectively. Upland and riparian site indices were correlated, but neither factor contributed to the best approximating models of salmonid biomass or fish length at age one, using all possible combinations of independent variables. Total salmonid biomass was best described by a positive relationship with drainage area. Length at age one was best described by a positive relationship with percentage of hardwoods within riparian areas. Percentage habitat saturation was not well described by any of the models constructed. The inability of upland or riparian forest productivity to predict salmonid productivity may reflect insufficient variation in independent variables, limitations of the metrics used to estimate productivity, and the operation of factors affecting salmonid production that are not subsumed in measures of forest productivity. The lack of a relationship between upland conifer and salmonid productivity suggests that management

of land for timber productivity and component streams for salmonid production in these sites will require separate, albeit integrated, management strategies.

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INTRODUCTION

Forest productivity is often defined in terms of site quality, which is measured by the maximum timber crop the land can produce in a given time (Daniel et al., 1979).

Among important abiotic factors contributing to site quality are climatic factors such as temperature and moisture, geologic features such as the type of parent material and orientation of bedrock, physical and chemical properties of soils, and physiography such as elevation, slope, aspect, land shape, and the land-water interface (Harlow et al., 1996).

These same features are also known to influence the carrying capacity of streams for salmonids. Water temperature, for example, affects salmonid growth rate, swimming ability, availability of dissolved oxygen, ability to capture and use food, and ability to withstand disease outbreaks (Reiser and Bjornn, 1979). It also affects the production of macroinvertebrates that form the salmonid prey base (Benke, 1993 and others). Physical habitat for salmonids is affected by channel morphology (Fukushima, 2001; Hicks and Hall, 2003). Channel morphology in turn reflects the interplay of climatically-driven hydrologic and geomorphic processes, including the recruitment of large woody debris.

Biotic factors also affect forest and stream productivity, however, and these may obscure or modify a relationship between forests and salmon. Biotic factors important in affecting forest productivity include plant competition, herbivory, pathogens, and anthropogenic activities that modify biotic processes. Competition, predation, pathogens, and anthropogenic activities also play a strong role in affecting salmonid production.

establish relationships between salmonid standing crops and in-stream habitat variables (Fausch et al., 1988; Inoue and Nakano, 2001 and others), or of restoration projects to improve salmonid production based on manipulation of physical variables alone (Gregory et al., 1987; Bisson and Bilby, 1998), may result from failures to address food availability.

While measurement of in-stream physical habitat often fails to account for food availability that is critical for assessing productive capacity of a stream, measurement of upland productivity subsumes at least some of the factors affecting food availability such as solar radiation and nutrients, as well as habitat elements. Thus, while it has often been difficult to establish relationships between salmonid production and in-stream habitat, one might see a correlation between upland productivity and salmonid productivity. Guyette and Rabeni (1995) reported significant correlations between annual growth increments of several tree species and rock bass Ambloplites rupestris in the Ozark Mountains. These growth increments, in turn, were correlated with climatic variables, including July rainfall and stream discharge. Although many studies have evaluated salmonid response to logging, (Hawkins et al., 1983; Bisson and Sedell, 1984; Hicks et al., 1991 and others), the spatial relationship between upland productivity and salmonid productivity in the Pacific Northwest does not appear to have been examined.

Although productivities of upslope forested stands and salmonids may be correlated, riparian condition may be a better predictor of juvenile salmonid productivity than upslope productivity. This is because of the key role riparian vegetation plays in providing an inflow of organic matter and influencing trophic pathways in streams

(Cummins et al., 1989). Riparian vegetation moderates air temperatures, provides bank stability, and provides a major source of large woody debris to a stream channel, which itself provides habitat, mediates channel topography, and stores sediments (Gregory et al., 1991). The main effect of riparian vegetation on stream productivity is likely due to litter inputs. Upland stand productivity may not be a good predictor of riparian condition, especially where the riparian zone is dominated by nitrogen-fixing red alder Alnus rubra.

The objective of this study was to quantify relationships between indices of salmonid productivity and forest stand productivity and (or) riparian condition in small coastal watersheds of northern California. Results are intended to contribute to an improved ability to characterize expected salmonid productivity, which is important for documenting impacts from management activities, and for establishing restoration targets for salmonid recovery.

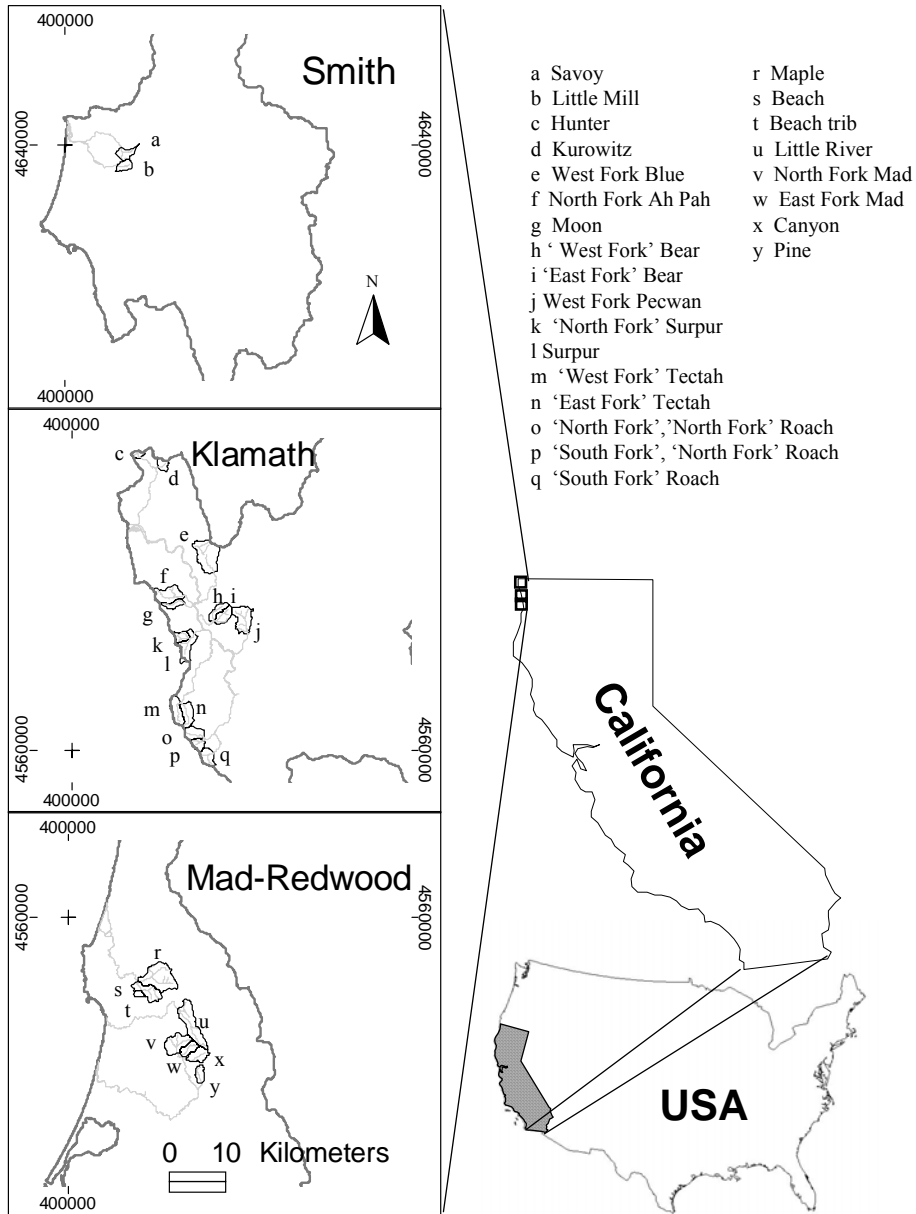
METHODS

Study Area

The relationship between upland productivity, riparian condition, and salmonid productivity was evaluated by analyzing data collected from twenty-five forest stands and their adjoining streams in coastal watersheds of northern California. Sites were located in small watersheds in the Smith River, Klamath River, Maple Creek, Little River, and Mad River drainages in Humboldt and Del Norte counties (Figure 1). The regional climate is characterized as marine west coast, with an annual average precipitation of 170-200 cm, approximately 75% of which falls as rain between November and March. Discharge in these basins during the period of sampling (October 2001 to September 2002) was slightly below average, based on 39 yrs of record (Freeman et al., 2003). Geology of the sites includes Mesozoic and Paleozoic metamorphic rocks, Mesozoic granitic rock, Mesozoic sedimentary rocks, and serpentized ultramafic rocks (Wagner, 2002).

The study was conducted on lands of Green Diamond Resource Company, in areas of second growth redwood Sequoia sempervirens and Douglas fir Pseudotsuga menziesii. Sites were selected to provide variation in Site Index values of the forest stands, with adjoining stream reaches in which the fish community was dominated by resident coastal cutthroat trout Oncorhynchus clarki clarki and rainbow/steelhead trout Oncorhynchus mykiss. Cutthroat and rainbow trout were chosen as the target species for analysis because they are present in streams year-round. Small numbers of juvenile coho

Figure 1. The 25 streams and their drainages studied in the Smith, Lower Klamath, and Mad-Redwood subwatersheds on the north California coast. Stream reaches surveyed were located at pour points of the corresponding watersheds.



salmon Oncorhynchus kisutch were observed in one stream. Other vertebrates present in the study sites included the coastal giant salamander Dicamptodon tenebrosus, tailed frog Ascaphus truei, and ammocoetes of Pacific lamprey Lampetra tridentata.

Stream reaches were generally located in 2nd and 3rd-order tributaries, with moderate gradients ranging from 2-9% slope, and catchments varying in size from 173-2233 hectares (Table 1). Study reach lengths were established using the proportional-distance designation (40 * avg stream width), a method adopted by the EMAP program and described in Barbour et al. (1999). Reach lengths averaged 125m and ranged from 60 to 200 m. Red alder was the dominant hardwood species found in the riparian areas along the reaches. Hardwood species present included red alder (42% of the total number of riparian trees), tanoak Lithocarpus densiflorus (11 %); Pacific myrtle Umbellularia californica (3%) and bigleaf maple Acer macrophyllum (2 %).

Upland forest productivity

Upland productivity was estimated using Site Index, which is the primary tool used worldwide in upland productivity estimation (Stearns-Smith, 2001). For a given tree species, Site Index is defined as the average tree height at some fixed age (commonly tree height at 50 yrs) attained by dominant and co-dominant site trees that are selected to reflect site potential. The height of dominant trees is used as the measure of productivity because, unlike timber volume, it is relatively unaffected by density except in extremely dense or sparse stands (Stearns-Smith, 2001). A different age-height model is required

Table 1. Stream reaches and attributes of upland and riparian areas selected as study sites. Upland Site Index (SI) was estimated for redwood and Riparian Site Index was estimated for red alder.

Creek	Basin	Reach	Riparian		% Riparian	Upland SI	Riparian SI	Drainage
		length (m)	width (m)	% Riparian hardwoods	canopy cover	Ht(ft) at age 50	Ht(ft) at age 50	area (ha)
Beach	Maple Creek	160	27	50	89	121	97	974
Beach tributary	Maple Creek	56	16	28	90	121	109	173
Canyon	Mad River	120	18	53	59	104	110	723
East Fork Bear	Klamath River	123	14	64	85	89	84	603
East Fork Mad	Mad River	80	14	34	85	109	109	536
East Fork Tectah	Klamath River	111	14	52	65	94	89	775
Hunter	Klamath River	87	15	74	89	98	101	224
Kurowitz	Klamath River	129	15	81	87	89	103	327
Little Mill	Smith River	200	16	63	81	94	100	413
Little River	Little River	120	11	54	42	111	93	1,817

Table 1. Stream reaches and attributes of upland and riparian areas selected as study sites. Upland Site Index (SI) was estimated for redwood and Riparian Site Index was estimated for red alder. (continued)

Creek	Basin	Reach	Riparian		% Riparian	Upland SI	Riparian SI	Drainage
		length (m)	width (m)	% Riparian hardwoods	canopy cover	Ht(ft) at age 50	Ht(ft) at age 50	area (ha)
Maple	Maple Creek	184	53	55	93	117	91	2,233
Moon	Klamath River	70	12	83	78	109	94	371
North Fork AhPah	Klamath River	164	17	41	90	114	110	1,163
North Fork Mad	Mad River	140	12	54	68	116	113	1,181
North Fork Surpur	Klamath River	98	14	57	83	117	106	404
North Fork,		75	15	49	80	106	92	652
North Fork Roach	Klamath River							
Pine	Mad River	80	17	84	78	114	100	417
Savoy	Smith River	200	16	77	86	114	103	505
South Fork Roach	Klamath River	120	15	48	71	103	88	636

Table 1. Stream reaches and attributes of upland and riparian areas selected as study sites. Upland Site Index (SI) was estimated for redwood and Riparian Site Index was estimated for red alder. (continued)

Creek	Basin	Reach	Riparian	% Riparian		Upland SI	Riparian SI	Drainage
		length (m)	width (m)	% Riparian hardwoods	canopy cover	Ht(ft) at age 50	Ht(ft) at age 50	area (ha)
South Fork,		94	16	57	85	102	93	397
North Fork Roach	Klamath River							
Surpur	Klamath River	135	17	71	83	115	104	961
West Fork Bear	Klamath River	90	14	76	87	101	103	486
West Fork Blue	Klamath River	118	19	61	81	81	85	1,876
West Fork Pecwan	Klamath River	168	16	29	86	90	81	1,244
West Fork Tectah	Klamath River	200	19	66	77	98	99	837

for each species because height growth patterns are not the same across species (Nigh, 1997). Site Index values are often grouped into five classes from the Site Index curves, with “I” being the highest and “V” being the lowest.

Site Index values of redwoods in upland areas of each watershed were obtained from Green Diamond Resource Company. The data for the Site Index values were obtained by cruise estimates, extrapolation from cruise estimates, field estimation, and photo interpretation. Values were field-verified by measuring tree height and coring dominant trees from 5 (20%) of the study sites. At each stream reach, four evenly spaced transects were established perpendicular to the channel. The dominant upland tree along each of the 4 transects, on each side of the channel ($n = 8$ trees per reach), was located by visual inspection. Because some transects did not contain a dominant or co-dominant tree due to crown damage or rocky soils, the number of trees cored per site for upland Site Index averaged 5.6. Upland was delimited as the region between the ridge top and the upslope edge of the riparian zone. Riparian width was determined for each transect by a change in uniform slope and vegetation type. Tree height was measured with a laser rangefinder and age was determined by coring trees with an increment borer. Averaged values were used to determine Site Index for the stand by using a look-up table from Hanson et al. (2003), which was modified from Krumland and Wensel (1977). Site Index look-up tables link tree height at present age with tree height at a common base age. Field measurements were only weakly correlated with data provided by Green Diamond Resource Company ($r = 0.13$). Because the field verification sample size was small and

the Green Diamond Resource Company data averaged values for the entire watershed, no adjustments were made to their dataset.

A small proportion of the catchment areas examined (avg = 12%) extended beyond lands within Green Diamond Resource Company ownership. These areas had similar land use as those on Green Diamond Resource Company property. Thus Site Index values supplied by Green Diamond Resource Company were assumed to apply to all uplands within the watershed boundaries. Drainage area was estimated by digitizing the watershed boundaries associated with corresponding stream reaches.

Riparian Condition

Riparian attributes measured at each site included the Site Index of red alder, riparian canopy composition (% hardwoods), and percentage canopy coverage. In five sites, Site Index of redwoods within the riparian area was measured to compare redwood Site Index between riparian and upland areas. In March 2003, following spring leaf-out of riparian hardwoods, measurements of each parameter were made along four evenly spaced transects perpendicular to the stream reach.

Percentage canopy cover was estimated using a spherical densiometer located 1.2 m above the water surface at the center of the channel width. Four readings (upstream, downstream, right bank, and left bank) were taken at each of the four transects and averaged together.

Canopy composition of riparian vegetation was quantified along both sides of the stream channel using a line transect and point intercept method (Bonham, 1989). Points

were established every two meters along transects extending to the edge of the riparian area. Percentage of hardwoods within the riparian zone was estimated as the number of point intercepts of hardwoods divided by total point intercept of all trees within the riparian canopy.

Alder Site Index was estimated from measurements of height and age of dominant or co-dominant individuals, if one was identified, located within each of the four riparian transects on each side of the stream (mean number of trees cored per site = 7). Tree height was measured with a laser rangefinder and age was determined by coring trees with an increment borer. Averaged values were used to determine alder Site Index at a base age of 50 yrs using tables and curves of Mitchell and Polsson (1988), which were modified from curves using an index age of 20 yrs by Harrington and Curtis (1986).

Salmonid Productivity

Unlike the Site Index for forest trees, however, standardized indices of productivity for salmonids have not been established. Warren (1971) defined productivity for salmonids as the capacity of a stream system to produce salmonid biomass irrespective of the prevailing rate of production. Production, defined as the product of growth rate and mean biomass over some time period, is strongly dependent on biomass as a result of density-dependent relationships between a consumer species and its limiting resources (Warren, 1971). Because of this, comparison of stream productivity for salmonids across streams is perhaps best evaluated using production curves which describe production at differing levels of biomass. However, this

information is not easily obtainable in natural systems, and requires both experimental manipulation of biomass and sequential sampling over time to estimate production. While recognizing limitations associated with instantaneous indices of productivity, measures were sought that were roughly analogous to site indices for forest stands. Three measures were chosen: total biomass (g/m^2), length of age 1 fish, and percentage habitat saturation.

Total biomass of salmonids was chosen as it represents a basic component in the estimation of production that integrates number and size of fish, and has been found to be a good indicator of stream habitat quality (Grant et al., 1986). Fish length at age 1 among the largest fish sampled was used as an estimate of productivity that is most analogous to the Site Index used for forest trees. As with trees, growth of the largest fish at a base age in the population may be relatively unaffected by population density (Keeley, 2001). Percentage habitat saturation was considered as an alternative index of population abundance that incorporates variation due to sampling date, size of fish, or growth rates between years (Grant et al., 1998). Percentage habitat saturation uses an allometric relationship between fish length and territory size to calculate habitat fullness as the percentage of the stream area occupied by the territories of salmonid fishes (Grant et al., 1998).

Fish were sampled once from each site during July - August 2002. Reaches were blocked with 6 mm mesh netting when natural barriers were not present. Samples were taken using multiple pass electroshocking. Each sampling included two or more passes until the number of fish removed was less than 20% of those removed during the

previous pass. Captured fish were anaesthetized with CO₂, identified, measured to the nearest millimeter fork length, weighed to the nearest 0.01 g, and allowed to recover before being released at the location of capture. At least fifty individuals of size-classes <90 mm and ≥90 mm of each species were measured and weighed. Scale samples for growth analysis were taken from ten of the largest fish within each reach. Due to an inability to reliably distinguish cutthroat, rainbow and steelhead trout and various hybrids; salmonids were grouped together for analysis.

Fish abundance was estimated using the Seber-LeCren and the Moran-Zippin estimators for two and more than two passes, respectively. The Seber-LeCren estimator (Seber, 1982) is described as:

$$\hat{N} = \frac{C_1}{1 - C_2 / C_1}, \quad (1)$$

where C_i = total number of fish collected in pass i. The Moran-Zippin estimator (Moran, 1951; Zippin, 1958) is described as:

$$\hat{N} = \frac{C}{1 - (1 - \hat{q})^n}, \quad (2)$$

where C = total number collected in all removals, n = total number of removals, and \hat{q} = estimated capture probability. Fish density was expressed as no. fish /m². Total biomass (g/m²) was estimated as mean mass of fish for each size class multiplied by that size class density.

Fish scales were analyzed using a compound microscope outfitted with a monochrome video camera and digitizing software. A magnification of 10X was used to

capture images. Measurements of scale annuli and radii were made within 10° of the long axis of the scales. Scale readings were verified by comparing 10% of the scales read ($n = 23$) to readings of a second reader. Precision, the coefficient of variation of the age estimated for each scale, was 3%. Fish length at age 1 was back-calculated using the Fraser-Lee formula (Fraser, 1916; Lee, 1920).

$$L_i = c + (L_c - c)\left(\frac{S_i}{S_c}\right), \quad (3)$$

where L_i = back-calculated fish body length at age i , L_c = fish body length at capture, S_i = mean scale length at annulus i , S_c = mean scale total length, c = intercept from the regression of body length on mean scale length. Values were averaged to determine mean length at age 1 for each reach.

Percentage habitat saturation was estimated as:

$$PHS = 100 \cdot \sum_{i=1}^n D_i \cdot T_i, \quad (4)$$

where D_i is the density (no./m²) of age class i and T_i is the territory size (m²) for age-class i . T_i was predicted from: \log_{10} territory size = 2.61 \log_{10} fork length (cm) - 2.83; Grant and Kramer, 1990. Fish were sorted into age classes from length-frequency analyses.

Statistical Analyses

Data were analyzed by constructing linear regression models with total salmonid biomass, length of age 1 fish, and percentage habitat saturation as separate response variables. Drainage area, percent riparian hardwoods, riparian (alder) Site Index, and

upland (redwood) Site Index were included as independent variables in all analyses. Drainage area was included because previous studies have found a relationship between drainage area and abundance and growth of salmonids (Kozel and Hubert, 1989; Harvey, 1998; Roni, 2002 and others). Riparian canopy coverage was omitted as an independent variable because perusal of the data showed that stream reaches varied little in canopy coverage (mean canopy coverage = 80%, SD = 11%). The set of candidate models for each dependent variable included all (15) combinations of the four independent variables. Transformations or interactions between independent variables were not included to reduce the risk of overfitting.

Sets of candidate models developed for each response variable were evaluated using Akaike's Information Criterion adjusted for small sample sizes (AIC_c), as recommended by Burnham and Anderson (2002). Models with AIC_c values within two units of the minimum AIC_c value were considered to be valid candidate models. Akaike weights (w_i) were used to evaluate the amount of evidence in favor of the specified model being the best actual model given the existing set of models.

RESULTS

Among independent variables, only riparian Site Index and upland Site Index were significantly correlated ($r = 0.54$; Figure 2). Redwood Site Index from upland areas was also strongly correlated with the redwood Site Index estimated from riparian areas ($r = 0.78$) although the sample size was only 5.

Among the salmonid response variables, correlations were seen between percentage habitat saturation and total biomass ($r = 0.74$) and between length at age 1 and total biomass ($r = 0.42$). Length at age 1 and percentage habitat saturation were not strongly correlated ($r = 0.08$). Summary data used in the estimation of stream productivity for salmonids is listed in Table 2.

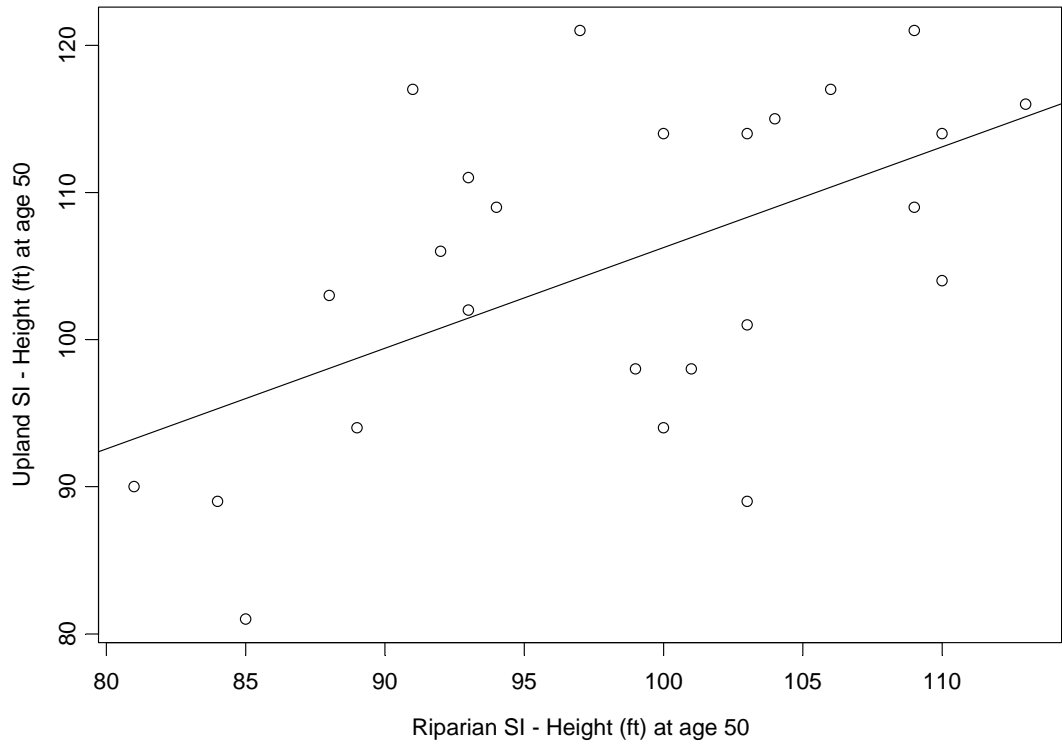


Figure 2. The relationship between Site Index of redwood in upland forest stands and Site Index for red alder in riparian areas.

Table 2. Density, total biomass, percent habitat saturation (PHS), and fork length at age 1 of salmonids sampled from the study sites.

Creek	Fish	Total	PHS	Length at age 1
	density	biomass		
	#/m ²	g/m ²	%	Mm
Beach	0.63	3.55	8.90	108
Beach tributary	0.93	2.73	16.07	83
Canyon	2.12	7.75	13.32	103
East Fork Bear	0.43	4.49	17.27	99
East Fork Mad	0.19	1.91	7.05	103
East Fork Tectah	0.30	1.63	7.88	109
Hunter	0.54	6.53	31.72	105
Kurowitz	0.82	8.75	25.65	120
Little Mill	0.12	1.19	6.24	NA
Little River	1.49	11.15	22.26	97
Maple	1.48	13.77	21.72	99
Moon	0.59	8.34	10.29	112
North Fork AhPah	0.46	5.71	16.50	104
North Fork Mad	0.14	1.22	5.45	97
North Fork Surpur	1.16	8.65	25.63	102
North Fork,				
North Fork Roach	0.89	6.72	31.68	89

Table 2. Density, total biomass, percent habitat saturation (PHS), and fork length at age 1 of salmonids sampled from the study sites. (continued)

Creek	Fish	Total	PHS	Length at age 1
	density	biomass		
	#/m ²	g/m ²	%	Mm
Pine	0.11	1.63	7.52	111
Savoy	0.22	1.03	5.88	NA
South Fork Roach	0.55	5.99	22.48	96
South Fork,				
North Fork Roach	0.27	3.09	14.95	94
Surpur	0.88	11.56	30.67	112
West Fork Bear	0.98	5.78	25.22	99
West Fork Blue	1.38	15.97	28.11	128
West Fork Pecwan	0.13	2.07	7.62	98
West Fork Tectah	0.20	1.11	5.75	NA

The positive relationship with drainage area provided the best approximating model for total biomass (Table 3, Figure 3). No other candidate models were within 2 AIC_c units of drainage area. The Akaike weight, 0.93, is large relative to the weight of the other models tested, and therefore, is strong evidence in favor of drainage area being the actual best fit model for total biomass of salmonids considering all the models.

For length at age 1, the positive relationship with percentage of hardwoods in riparian areas provided the best-approximating model (Table 3, Figure 3) with no other models within 2 AIC_c units. The Akaike weight of 0.89 is strong evidence the percentage of hardwoods model is likely the best.

None of the models represented percentage habitat saturation well, due to the low coefficient of determinations for each of the models (Table 3). Relationships of drainage area and percentage of hardwoods in riparian areas to percentage habitat saturation were positive. Riparian Site Index and upland Site Index were negatively related to percentage habitat saturation.

Table 3. The best approximating models of relationships between salmonid response variables, and habitat characteristics in 25 watersheds in coastal northern California, as measured by AICc. PHS = percent habitat saturation. SI = Site Index. The influence of independent variables on salmonid response (+)(-), the coefficient of determination (r^2), differences in AICc between models (Δ_i), and Akaike weights (ω_i) are shown. Models within 2 AICc units of the best model are shown.

Salmonid				
Productivity	Habitat Variables	r^2	Δ_i	ω_i
Total Biomass	drainage area (+)	0.29	0.00	0.93
Length at Age 1	hardwoods (+)	0.30	0.00	0.89
PHS	hardwoods (+)	0.02	0.00	0.28
	upland SI (-)	0.01	0.27	0.24
	riparian SI (-)	0.01	0.31	0.24
	drainage area (+)	0.01	0.36	0.23

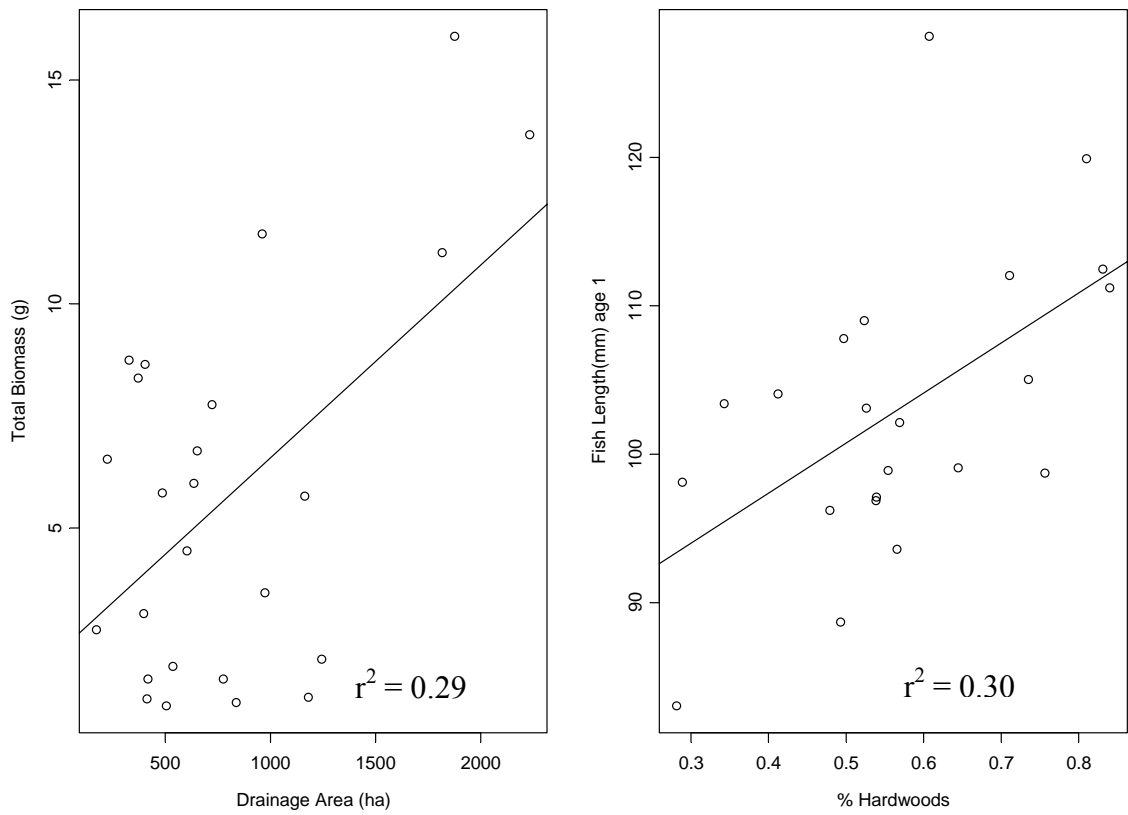


Figure 3. The best –approximating models of total salmonid biomass and length at age 1 in 25 watersheds of coastal northern California among a set of candidate models that included all combinations of independent variables quantifying drainage area, percent riparian hardwoods, and riparian (alder) and upland (redwood) Site Index values.

DISCUSSION

In this study, Site Indexes of upland redwood and riparian red alder were moderately correlated, but neither Site Index accurately predicted salmonid productivity. The correlation of Site Index between upland and riparian areas likely reflects generally similar environmental requirements of red alder and redwood. Perhaps why the correlation was not stronger may be due to the greater sensitivity of red alder growth to light and soil moisture conditions (Chan et al., 2003); and the independence of alder growth from soil nitrogen levels. The latter stems from the nitrogen-fixing ability of red alder through symbiotic actinomycetes (Hibbs et al., 1994). Failure of either riparian or upland Site Index to predict salmonid productivity may reflect: 1) insufficient variation in the independent variables, 2) limitations of measurements used to estimate productivities of both trees and fish, and 3) the operation of other factors limiting salmonid production that are not encompassed in measures of forest productivity.

Despite efforts to select stream reaches under private ownership in coastal northern California that exhibited a large range in upland Site Index, most of the watershed areas averaged to Site Class II and III. The lack of a large range in Site Index likely contributed to an inability to ascertain a relationship between forest and salmonid productivities that might exist among watersheds with greater extremes in Site Index, or at larger spatial scales. For example, in a study of 13 streams of southeastern Minnesota, Kwak and Waters (1997) were unable to find a relationship between production of brook trout Salvelinus fontinalis and water quality variables. However, when the analysis was

supplemented with more variable data from across the United States, a strong correlation was observed between regional brook trout production and alkalinity. This suggests a need to expand the spatial scale of investigation in future research on the relationship between forest and fish production. Within the Pacific Northwest ecoregion, greater variation in forest productivity is likely to be achieved by expanding the longitudinal (i.e. distance inland from the coast) rather than the latitudinal boundaries of investigation.

Apart from insufficient variation in Site Index values, limitations of the measurements used to estimate forest and fish productivities may obscure a potential relationship. Site Index is the industry standard for estimating forest site productivity worldwide. However, selection of site trees that do not accurately reflect site potential and measurement error may result in spurious conclusions about site productivity. Site Index can be measured directly only when stands are at index age. Site trees are assumed to have experienced unrestrained height growth, free from past effects of suppression, repression, and damage from insects, disease, and weather. However, past histories may be unknown and existing stand conditions may not produce suitable site trees. Use of height growth curves and tables to estimate site quality are likely to be less accurate (Harrington and Curtis 1986), particularly when stands are young. Small errors in height measurements of young trees can cause large errors in Site Index estimates. The low correlation observed in this study between Site Index values provided by Green Diamond Resource Company and those obtained by ground-truthing from 20% of the study sites may reflect measurement error, but are probably largely attributable to differences in sample size and area over which site trees were selected. Site Index values

provided by the timber company were averaged over the entire watershed immediately above the study reaches, while values obtained by ground-truthing were obtained from measurement of trees growing along transects perpendicular to the stream reach.

Limitations associated with measurements chosen to represent the capacity of a stream system to produce salmonids may be more problematic than those associated with use of Site Index to estimate forest productivity. For example, biomass and percentage habitat saturation are both instantaneous measures that reflect only current conditions within the stream reach rather than the reach potential to support salmonid production. Salmonid biomass provides a measure of the existing standing crop that is supported in a stream reach, but depending on the size/age structure of the population, greatly differing amounts of production can be achieved from similar standing crops. Large biomass does not necessarily result from high productivity when, for example, there is a small number of large individuals. Nor does small biomass necessarily result from low productivity. Use of biomass as a surrogate for salmonid productivity may be particularly problematic in this study, as the relative proportion of resident vs. anadromous individuals within the population was unknown. This is relevant in that anadromous fish that do not reside in a stream reach year-round may not require the same array of resources provided by the habitat as do resident individuals.

Unknown proportions of resident and anadromous individuals also compromise the appropriateness of length of fish at age 1 as a measure of salmonid productivity. Anadromous individuals may exhibit more rapid growth as juveniles than do stream-resident forms. Nonetheless, this measurement offers intuitive appeal as a measure that is

most closely analogous to the conceptual underpinning of the Site Index, and as one that is expressed per unit of time. Correlative and experimental studies of stream salmonids have shown that large, aggressive individuals are able to monopolize food resources by occupying and successfully defending the most profitable habitat areas (Grant, 1990; Nielsen, 1992; Keeley, 2001), thus supporting the Site Index assumption that growth attained by dominant individuals may be relatively unaffected by density. As with the Site Index, errors in selection of dominant individuals and dependence of growth on conditions during the temporal period of measurement contribute to imprecision of the measure.

Percentage habitat saturation is a relatively recent measure that has been suggested as a preferable alternative to the use of population density as an index of salmonid abundance, because it incorporates important variation due to sampling date, size of fish, or growth rates between years (Grant et al., 1998). For example, declines in fish density observed in sequential sampling may give a false impression of a decrease in population abundance if the density decline is balanced by an increase in the spatial requirements of surviving, larger individuals. Assuming that a population is at carrying capacity and that territory size is a functional predictor of the space required by a salmonid fish; percentage habitat saturation is useful as a measure of stream productivity for salmonids in that it potentially suggests how much of the habitat is suitable for supporting salmonids. A percentage habitat saturation of 100 would indicate that salmonids occupied territories covering the surface area of the stream bottom. The major limitations of percentage habitat saturation approach lie in validity of the assumptions.

Demonstration that a population is at carrying capacity is a formidable challenge requiring long-term monitoring and (or) manipulation of fish density. The assumption that territory size is a useful predictor of spatial requirements in turn assumes that minimum territory sizes are inflexible, and is contraindicated by data showing changes in territory size with changes in food abundance (Keeley and McPhail, 1998; Keeley, 2000), although not necessarily in direct proportion (Keeley, 2001).

While none of the measures of salmonid productivity showed a relationship with riparian or upland productivity, a positive relationship was demonstrated between total salmonid biomass and drainage area. This supports findings of previous studies, but the explanation for the pattern is not clear. For example, Harvey (1998) observed higher downstream growth of resident cutthroat trout in a northern California stream. Fish are likely not responding to drainage area per se, but rather to discharge and (or) resource supply. As basin size increases, the channel length and area that are affected by confluence effects are predicted to increase (Benda et al., 2004). Morphologically diverse tributary junctions may produce increased spatial and temporal heterogeneity in resources and habitat, and thus provide an explanation for an increase in fish biomass with drainage area. Alternatively, as basin size increases, the network of small headwater (perennial and intermittent) stream channels supplying energy and matter to receiving reaches is also likely to increase. If this is true, one might expect a positive correlation between salmonid production and number of tributary junctions. Longitudinal gradients in temperature, which affect both fish bioenergetics and secondary production, may also explain increases in salmonid production with drainage area.

Of the three measures chosen to estimate stream productivity for salmonids, only fish length at age 1 showed a modest correlation with any of the variables describing riparian/upland attributes. Data suggested that potential growth of fish increases with an increase in the percentage of hardwoods in riparian areas. As red alder was the dominant riparian hardwood tree, one explanation for this may lie in the increased provisioning of nitrogen to stream reaches as a consequence of nitrogen fixation by alder. Recent studies in coastal Oregon (Compton et al., 2003) and southeastern Alaska (Piccolo and Wipfli, 2002) have shown strong correlations between the percentage of alder within a watershed and surface water concentrations of nitrate. As nitrogen appears to be a limiting nutrient for benthic primary production in streams in northern California (Triska et al., 1983; Ambrose et al., 2004), increased concentrations may increase primary production, with cascading effects through the food web. When nutrients are in short supply, primary production may be reduced, resulting in reduced availability of invertebrate prey and slower fish growth. Other factors such as light availability may interact with nutrient supply in affecting primary production and fish growth (Wilzbach et al., 2005). Further research on interactions between alder-associated shading and nutrient dynamics in affecting salmonid growth and supporting trophic pathways is warranted.

A second possible explanation for an increase in fish growth with an increase in the percentage of riparian hardwoods (alder) lies in the provisioning of litter inputs to stream reaches, which may support salmonid growth through heterotrophic pathways. Litter input from hardwood trees is more quickly conditioned and made available for

invertebrate consumption than is litter input from conifers (Cummins et al., 1989; Cummins, 2002), and may support a greater biomass of invertebrate prey. Provisioning of nutrients and provisioning of litter input are not mutually exclusive explanations that might account for the relationship between percentage of riparian hardwoods and salmonid growth. Salmonid growth probably derives from autotrophic pathways during spring and summer periods of active growth (Bisson and Bilby, 1998), but body mass may be maintained during winter from heterotrophic pathways. Preliminary research findings from a comparison of alder vs. conifer-dominated stream systems in the Olympic Peninsula (Volk, 2004) support the possibility that nutrient and (or) litter subsidies from red alder underlie a positive correlation between salmonid growth and percentage of riparian hardwoods. Both a higher biomass of benthic and drifting invertebrates and possibly higher levels of specific essential fatty acids in fish were found in alder-dominated systems. In my study, although the percentage of riparian hardwoods was related to fish length at age 1, it was not related to either total salmonid biomass or percentage habitat saturation. This may be explained if hardwood-associated food resources were monopolized by dominant individuals that suppressed the growth of sub-dominants, or if regulation of salmonid populations was expressed through density-dependent mortality or emigration rather than growth.

The relative contribution of mortality, emigration, and growth to population regulation in stream-dwelling salmonids has not been established (Keeley 2001), nor has been a related determination of whether stream salmonids are limited primarily by space or by food,

despite decades of inquiry (Chapman 1966). Bisson and Bilby (1998) have argued that the large world-wide variation in stream salmonid production appears to be attributable primarily to differences in food abundance. Salmonid production in natural systems is greatest in hardwater streams with relatively high inorganic nutrient concentrations, moderate temperatures, and relatively low vegetative canopy coverage allowing ample sunlight to reach streams, irrespective of habitat features. The highest salmonid production of all is achieved in hatcheries, which offer abundant food but virtually no habitat. But production is achieved only if individuals survive, and survival is certainly dependent on habitat features that offer refuge from predators and natural disturbances. It is probably naive to believe that either food or space might exclusively limit salmonid production. Many factors potentially limit salmonid production that are not adequately encompassed in measures of forest productivity. For example, temperature regime and the amount of solar radiation available to upslope vegetation are factors likely affecting Site Index values. But their incorporation into Site Index may not adequately express either the incident radiation received by a stream or its temperature regime, because of the large moderating role played by riparian cover and topographic shading, particularly in small stream settings (Poole and Berman, 2001).

Timber companies are primarily interested in upslope production of conifers. As this study found no evidence of a relationship between upslope conifer productivity and salmonid productivity, an implication is that, at least in these sites, the management of land for timber productivity and component streams for salmonid production will require

separate, albeit integrated, management strategies. Thus, whether harvest is of trees from good or poor quality sites may have little direct consequence for salmonid populations in the streams that flow through these sites.

LITERATURE CITED

- Ambrose, H.A., Wilzbach, M.A., Cummins, K.W., 2004. Periphyton response to increased light and salmon carcass introduction in northern California streams. *J. N. Am. Benthol. Soc.* 23, 701-712.
- Barbour, M.T., Gerritsen, J., Snyder, B.D., Stribling, J.B., 1999. Rapid bioassessment protocols for use in streams and wadeable rivers: periphyton, benthic macroinvertebrates, and fish. Second Edition, EPA 841-B-99-002. Office of Water, U.S. Environmental Protection Agency, Washington, D.C.
- Benda, L., Miller, D., Dunne, T., Poff, L., Reeves, G., Pess, G., Pollock M., 2004. Network disturbance theory: how channel networks structure river habitats, *BioScience* 54, 413-428.
- Benke, A.C., 1993. Concepts and patterns of invertebrate production in running waters. *Verh. Int. Ver. Theor. Ang. Limnol.* 25, 15-38.
- Bisson, P.A., Bilby, R.E., 1998. Organic matter and trophic dynamics. In: Naiman, R.J., Bilby, R.E. (Eds.), *River Ecology and Management: Lessons from the Pacific Coastal Ecoregion*. Springer, New York, pp. 373-392.
- Bisson, P.A., Sedell, J.R., 1984. Salmonid populations in streams in clearcut versus old-growth forests of western Washington. In: Meehan, W.R., Merrell, T.R. Jr., Hanley, T.A. (Eds.), *Proceedings, Fish and Wildlife Relationships in Old-Growth Forests Symposium*. American Institute of Fishery Research Biologists, Asheville, NC, pp. 121-129.
- Bonham, C.D., 1989. *Measurements of Terrestrial Vegetation*. John Wiley and Sons, New York.
- Burnham, K.P., Anderson, D.R., 2002. *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. Springer, New York.
- Chan, S.S., Radosevich, S.R., Grotta, A.T., 2003. Effects of contrasting light and soil moisture availability on the growth and biomass allocation of Douglas-fir and red alder. *Can. J. For. Res.* 33, 106-117.

- Chapman, D.W., 1966. Food and space as regulators of salmonid populations in streams. *Am. Nat.* 100, 345-357.
- Compton, J.E., Church, M.R., Larned, S.T., Hogsett, W.E., 2003. Nitrogen export from forested watersheds in the Oregon Coast Range: The role of N₂-fixing red alder. *Ecosystems* 6, 773-785
- Cummins, K.W. 2002. Riparian-stream linkage paradigm. *Verh. Internat. Verein. Limnol.* 28, 49-58.
- Cummins, K.W., Wilzbach, M.A., Gates, D.M., Perry, J.B., Taliaferro, W.B., 1989. Shredders and riparian vegetation. *Bioscience* 39(1), 24-30.
- Daniel, T.W., Helms, J.A., Baker, F.S., 1979. *Principles of Silviculture*, 2nd edition. McGraw-Hill, New York.
- Fausch, K.D., Hawkes, C.L., Parsons, M.G., 1988. Models that predict standing crop of stream fish from habitat variables. General Technical Report. PNW-GTR-213. US Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, OR.
- Fraser, C.M., 1916. Growth of the spring salmon. *Trans. Pacific Fish. Soc.* 2 (1915), 29-35.
- Freeman, L.A., Smithson, J.R., Webster, M.D., Pope, G.L., Friebel, M.F., 2003. Water Resources Data – California, Water Year 2002, Volume 2. Pacific Slope Basins from Arroyo Grande to Oregon State Line except Central Valley, USGS-WDR-CA-02-2. U.S. Geological Survey, Water Resources Division, California District.
- Fukushima, M., 2001. Salmonid habitat-geomorphology relationships in low-gradient streams. *Ecology* 82, 1238-1246.
- Grant, J.W.A., 1990. Aggressiveness and the foraging behaviour of young-of-the-year brook charr (*Salvelinus fontinalis*). *Can. J. Fish. Aquat. Sci.* 47, 915–920.
- Grant, J.W.A., Englert, J., Bietz, B.F., 1986. Application of a method for assessing the impact of watershed practices: Effects of logging on salmonid standing crops. *N. Am. J. Fish. Manage.* 6, 24-31.
- Grant, J.W.A., Kramer, D.L., 1990. Territory size as a predictor of the upper limit to population density of juvenile salmonids in streams. *Can. J. Fish. Aquat. Sci.* 47, 1724-1737.

- Grant, J.W.A., Steingrímsson, S.Ó., Keeley, E.R., Cunjak, R.A., 1998. Implications of territory size for the measurement and prediction of salmonid abundance in streams. *Can. J. Fish. Aquat. Sci.* 55(Suppl. 1), 181-190.
- Gregory, S.V., Lamberti, G.A., Erman, D.C., Koski, K.V., Murphy, M.L., Sedell, J.R., 1987. Influence of Forest Practices on Aquatic Production. In: Salo, E.O., Cundy, T.W. (Eds.), *Streamside Management: Forestry and Fishery Interactions. Contribution 57*, Institute of Forest Resources, University of Washington, Seattle, WA., pp. 233-255.
- Gregory, S.V., Lamberti, G.A., Moore, K.M.S., 1989. Influence of valley floor land forms on stream ecosystems. In: Abell, D.L. (Ed.), *Proceedings of the California Riparian Systems Conference: Protection, Management, and Restoration for the 1990s*, Conference held 22-24 September 1988, Davis, California. General Technical Report PSW-110, US Department of Agriculture, Forest Service, Pacific Southwest Forest and Range Experiment Station, Berkeley, CA., pp. 3-8.
- Gregory, S.V., Swanson, F.J., McKee W.A., 1991. An ecosystem perspective of riparian zones. *BioScience* 40, 540-551.
- Guyette, R.P., Rabeni C.F., 1995. Climate response among growth increments of fish and trees. *Oecologia* 104(3), 272-279.
- Hanson, E.J., Azuma, D.L. Hiserote, B.A., 2003. Site Index equations and mean annual increment equations for Pacific Northwest Research Station Forest Inventory and Analysis Inventories, 1985-2001. Research Note PNW-RN-533. US Department of Agriculture, Forest Service, Pacific Northwest Research Station. Portland, OR.
- Harlow, W.M., Harrar, E.S., Hardin, J.W., White F.M., 1996. *Textbook of dendrology*, 8th edition. McGraw-Hill, New York.
- Harrington, C.A., Curtis, R.O., 1986. Height growth and Site index curves for red alder. Research Paper PNW-358. US Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, OR.
- Harvey, B.C., 1998. Influence of large woody debris on retention, immigration, and growth of coastal cutthroat trout (*Oncorhynchus clarki clarki*) in stream pools. *Can. J. Fish. Aquat. Sci.* 55, 1902-1908.
- Hawkins, C.P., Murphy, M.L., Anderson, N.H., Wilzbach, M. A., 1983. Density of fish and salamanders in relation to riparian canopy and physical habitat in streams of the northwestern United States. *Can. J. Fish. Aquat. Sci.* 40, 1173-1185.

- Hibbs, D.E., DeBell, D.S., Tarrant, R.F., 1994. N₂-Fixing Abilities of Red Alder: The Biology and Management of Red Alder. Oregon State University Press, Corvallis, OR.
- Hicks, B.J., Hall, J.D., 2003. Rock type and channel gradient structure salmonid populations in the Oregon Coast Range. *Trans. Am. Fish. Soc.* 132, 468-482.
- Hicks, B.J., Hall, J.D., Bisson, P.A., Sedell, J.R., 1991. Responses of Salmonids to Habitat Changes. *Am. Fisheries Soc. Spec. Pub. No. 19*, Bethesda, MD, pp. 483-518.
- Inoue, M., Nakano, S., 2001. Fish abundance and habitat relationships in forest and grassland streams, northern Hokkaido, Japan. *Ecol. Res.* 16, 233-247.
- Keeley, E.R., 2000. An experimental analysis of territory size in juvenile steelhead trout. *Anim. Behav.* 59, 477-490.
- Keeley, E.R., 2001. Demographic responses to food and space competition by juvenile steelhead trout. *Ecology* 82, 1247-1259.
- Keeley, E.R., McPhail, J.D., 1998. Food abundance, intruder pressure, and body size as determinants of territory size in juvenile steelhead trout (*Oncorhynchus mykiss*). *Behaviour* 135, 65-82.
- Kozel, S.J., Hubert, W.A., 1989. Factors influencing the abundance of brook trout (*Salvelinus fontinalis*) in forested mountain streams. *J. Freshwat. Ecol.* 5, 113-122.
- Krumland, B., Wensel, L., 1977. Height growth patterns and fifty year base age site index curves for young growth coastal redwood. Res. Note 4. University of California, College of Natural Resources, Co-op Redwood Yield Research Project, Berkeley, CA.
- Kwak, T.J., Waters, T.F., 1997. Trout production dynamics and water quality in Minnesota streams. *Trans. Am. Fish. Soc.* 126, 35-48.
- Lee, R.M., 1920. A review of the methods of age and growth determination in fishes by means of scales. *Fish. Invest. Lond. Ser. 2*, 4(2):1-32.
- Mitchell, K.J., Polsson, K.R., 1988. Site index curves and tables for British Columbia: coastal species. FRDA Report 37. Canadian Forestry Service and British Columbia Ministry of Forests, Victoria, B.C.
- Moran, P.A.P., 1951. A mathematical theory of animal trapping. *Biometrika* 38, 307-311.

- Nielsen, J.L., 1992. Microhabitat-specific foraging behavior, diet and growth rates in juvenile coho salmon. *Trans. Am. Soc. Fish.* 121, 617-634.
- Nigh, G.D., 1997. A Sitka spruce height-age model with improved extrapolation properties. *For. Chron.* 73, 363-369.
- Piccolo, J.J., Wipfli, M.S., 2002. Does red alder (*Alnus rubra*) in upland riparian forests elevate macroinvertebrate and detritus export from headwater streams to downstream habitats in southeastern Alaska? *Can. J. Fish. Aquat. Sci.* 59, 503-513.
- Poole, G.C., Berman, C.H., 2001. An ecological perspective on in-stream temperature: natural heat dynamics and mechanisms of human-caused thermal degradation. *Environ. Manage.* 27, 787-802.
- Reiser, D.W., Bjornn, T.C. 1979. Influence of forest and rangeland management on anadromous fish habitat in the western United States and Canada. Part 1: Habitat requirements of anadromous salmonids. General Technical Report PNW-96. US Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experimental Station, Portland, OR.
- Roni, P., 2002. Habitat use by fishes and Pacific giant salamanders in small western Oregon and Washington streams. *Trans. Am. Fish. Soc.* 131, 743-761.
- Seber, G.A.F., 1982. The estimation of animal abundance and related parameters, 2nd edition. MacMillan, New York.
- Stearns-Smith, S., 2001. Making sense of site index estimates in British Columbia: A quick look at the big picture. *B.C. Journal of Ecosystems and Management.* 1(1).
- Triska, F.J., Kennedy, V.C., Avanzino, R.J., Reilly, B.N., 1983. Effect of simulated canopy cover on regulation of nitrate uptake and primary production by natural periphyton assemblages. In: Fontaine, T.D. III, Bartell, S.M. (Eds.), *Dynamics of Lotic Ecosystems*. Ann Arbor Science, Ann Arbor, MI. pp. 129-159.
- Volk, C. 2004. Red alder on the rise - making a comeback both economically and ecologically. *Watershed Rev.* 2, 4-5.
- Wagner, D.L., 2002. Generalized Geologic Map of California, Note 17. California Department of Conservation, California Geological Survey.
- Warren, C.E., 1971. *Biology and Water Pollution Control*. Saunders, Philadelphia.

Wilzbach, M.A., Harvey, B.C., White, J.L., Nakamoto, R.J., 2005. Effects of riparian canopy opening and salmon carcass addition on the abundance and growth of resident salmonids. *Can. J. Fish. Aquat. Sci.*, in press.

Zippin, C., 1958. The removal method of population estimation. *J. Wildl. Manage.* 22, 82–90.

Appendix A. Site Index table for redwood sprouts from Hanson et al. (2003), modified from Krumland and Wensel (1977).

Breast		Redwood Site Index											
height													
age													
(yrs)	50	60	70	80	90	100	110	120	130	140	150	160	
	Top height (Ft)												
10	17	19	22	24	26	28	30	32	34	36	39	42	
15	22	26	29	33	37	40	44	48	52	56	60	64	
20	27	32	37	41	46	51	56	61	67	72	78	83	
25	31	37	43	49	55	61	67	74	80	86	93	100	
30	35	42	49	56	63	70	77	85	92	99	107	114	
35	39	47	55	63	71	78	86	95	103	111	119	127	
40	43	52	60	69	77	86	95	104	113	121	130	139	
45	47	56	65	75	84	93	103	112	122	131	141	150	
50	50	60	70	80	90	100	110	120	130	140	150	160	
55	53	64	75	85	96	106	117	127	138	148	159	169	
60	56	68	79	90	101	112	123	134	145	156	167	178	
65	59	71	83	94	106	118	129	140	152	163	174	185	
70	62	74	87	99	111	123	135	146	158	170	181	193	
75	65	78	90	103	115	128	140	152	164	176	188	199	
80	67	81	94	107	120	132	145	157	169	182	194	206	
85	70	84	97	110	124	136	149	162	175	187	199	211	
90	72	86	100	114	127	141	154	167	179	192	205	217	
95	75	89	103	117	131	144	158	171	184	197	209	222	

Appendix A. Site Index table for redwood sprouts from Hanson et al. (2003), modified from Krumland and Wensel (1977). (continued)

Breast height age (yrs)	Redwood Site Index											
	50	60	70	80	90	100	110	120	130	140	150	160
	Top height (Ft)											
100	77	92	106	120	134	148	162	175	188	201	214	227
105	79	94	109	123	138	152	165	179	192	205	218	231
110	81	96	111	126	141	155	169	182	196	209	222	235
115	83	99	114	129	143	158	172	186	199	213	226	239
120	85	101	116	131	146	161	175	189	203	216	230	243
125	87	103	119	134	149	164	178	192	206	219	233	246
130	88	105	121	136	151	166	181	195	209	223	236	249
135	90	107	123	138	154	169	183	198	212	225	239	252
140	92	109	125	141	156	171	186	200	214	228	242	255
145	93	110	127	143	158	173	188	202	217	231	244	258
150	95	112	128	145	160	175	190	205	219	233	247	260
155	96	114	130	146	162	177	192	207	221	235	249	262
160	98	115	132	148	164	179	194	209	223	237	251	264
165	99	117	133	150	166	181	196	211	225	239	253	266
170	100	118	135	151	167	183	198	213	227	241	255	268
175	102	119	136	153	169	184	200	214	229	243	257	270
180	103	121	138	154	170	186	201	216	230	244	258	272
185	104	122	139	156	172	188	203	217	232	246	260	273
190	105	123	140	157	173	189	204	219	233	247	261	275

Appendix A. Site Index table for redwood sprouts from Hanson et al. (2003), modified from Krumland and Wensel (1977). (continued)

Breast		Redwood Site Index											
height													
age													
(yrs)	50	60	70	80	90	100	110	120	130	140	150	160	
													Top height (Ft)
195	106	124	142	158	175	190	205	220	235	249	263	276	
200	107	125	143	160	176	192	207	222	236	250	264	277	

Appendix B. Site Index table for second-growth coastal red alder from Mitchell and Polsson (1988), modified from Harrington and Curtis (1986). bh = Breast height.

bh age (yrs)	Red alder Site Index																				
	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
	Top height (m)																				
10	7.6	8.1	8.6	9.3	9.9	10.5	11.2	11.9	12.7	13.5	14.3	15.2	16.1	17.0	18.0	19.0	20.0	21.1	22.1	23.3	24.4
11	8.1	8.6	9.2	9.9	10.5	11.2	12.0	12.7	13.5	14.3	15.2	16.1	17.0	18.0	19.0	20.0	21.1	22.2	23.3	24.5	25.6
12	8.6	9.2	9.8	10.5	11.2	11.9	12.7	13.4	14.3	15.1	16.0	17.0	17.9	19.0	20.0	21.0	22.1	23.2	24.4	25.6	26.7
13	9.0	9.7	10.3	11.0	11.8	12.5	13.3	14.1	15.0	15.9	16.8	17.8	18.8	19.8	20.9	22.0	23.1	24.2	25.4	26.6	27.8
14	9.5	10.2	10.9	11.6	12.3	13.1	14.0	14.8	15.7	16.6	17.6	18.6	19.6	20.7	21.7	22.9	24.0	25.1	26.3	27.5	28.7
15	10.0	10.7	11.4	12.1	12.9	13.7	14.6	15.5	16.4	17.3	18.3	19.3	20.4	21.5	22.6	23.7	24.8	26.0	27.2	28.4	29.6
16	10.4	11.1	11.9	12.7	13.5	14.3	15.2	16.1	17.0	18.0	19.0	20.0	21.1	22.2	23.3	24.5	25.6	26.8	28.0	29.2	30.4
17	10.8	11.6	12.3	13.2	14.0	14.8	15.7	16.7	17.6	18.6	19.6	20.7	21.8	22.9	24.0	25.2	26.4	27.5	28.8	30.0	31.2
18	11.3	12.0	12.8	13.6	14.5	15.4	16.3	17.2	18.2	19.2	20.3	21.3	22.4	23.6	24.7	25.9	27.1	28.2	29.5	30.7	31.9
19	11.7	12.4	13.2	14.1	15.0	15.9	16.8	17.8	18.8	19.8	20.9	21.9	23.0	24.2	25.3	26.5	27.7	28.9	30.1	31.4	32.6
20	12.1	12.9	13.7	14.6	15.4	16.4	17.3	18.3	19.3	20.3	21.4	22.5	23.6	24.8	25.9	27.1	28.3	29.5	30.7	32.0	33.2
21	12.4	13.3	14.1	15.0	15.9	16.8	17.8	18.8	19.8	20.9	21.9	23.0	24.2	25.3	26.5	27.7	28.9	30.1	31.3	32.5	33.7
22	12.8	13.6	14.5	15.4	16.3	17.3	18.3	19.3	20.3	21.4	22.5	23.6	24.7	25.9	27.0	28.2	29.4	30.6	31.8	33.0	34.3
23	13.2	14.0	14.9	15.8	16.7	17.7	18.7	19.7	20.8	21.8	22.9	24.0	25.2	26.3	27.5	28.7	29.9	31.1	32.3	33.5	34.7

Appendix B. Site Index table for second-growth coastal red alder from Mitchell and Polsson (1988), modified from Harrington and Curtis (1986). bh = Breast height. (continued)

bh age (yrs)	Red alder Site Index																				
	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
	Top height (m)																				
24	13.5	14.4	15.3	16.2	17.2	18.1	19.1	20.2	21.2	22.3	23.4	24.5	25.6	26.8	28.0	29.2	30.4	31.5	32.8	34.0	35.2
25	13.9	14.7	15.6	16.6	17.5	18.5	19.6	20.6	21.6	22.7	23.8	24.9	26.1	27.3	28.4	29.6	30.8	32.0	33.2	34.4	35.6
26	14.2	15.1	16.0	17.0	17.9	18.9	19.9	21.0	22.0	23.1	24.2	25.4	26.5	27.7	28.8	30.0	31.2	32.4	33.6	34.8	36.0
27	14.5	15.4	16.4	17.3	18.3	19.3	20.3	21.4	22.4	23.5	24.6	25.8	26.9	28.1	29.2	30.4	31.6	32.8	33.9	35.2	36.3
28	14.8	15.8	16.7	17.7	18.6	19.7	20.7	21.7	22.8	23.9	25.0	26.1	27.3	28.4	29.6	30.8	31.9	33.1	34.3	35.5	36.7
29	15.1	16.1	17.0	18.0	19.0	20.0	21.0	22.1	23.2	24.3	25.4	26.5	27.6	28.8	29.9	31.1	32.3	33.4	34.6	35.8	37.0
30	15.4	16.4	17.3	18.3	19.3	20.3	21.4	22.4	23.5	24.6	25.7	26.8	28.0	29.1	30.3	31.4	32.6	33.7	34.9	36.1	37.2
31	15.7	16.7	17.6	18.6	19.6	20.7	21.7	22.8	23.8	24.9	26.0	27.2	28.3	29.4	30.6	31.7	32.9	34.0	35.2	36.4	37.5
32	16.0	17.0	17.9	18.9	19.9	21.0	22.0	23.1	24.2	25.2	26.4	27.5	28.6	29.7	30.9	32.0	33.2	34.3	35.4	36.6	37.7
33	16.3	17.3	18.2	19.2	20.2	21.3	22.3	23.4	24.5	25.5	26.7	27.8	28.9	30.0	31.1	32.3	33.4	34.5	35.7	36.8	38.0
34	16.6	17.5	18.5	19.5	20.5	21.6	22.6	23.7	24.7	25.8	26.9	28.0	29.2	30.3	31.4	32.5	33.7	34.8	35.9	37.1	38.2
35	16.8	17.8	18.8	19.8	20.8	21.8	22.9	24.0	25.0	26.1	27.2	28.3	29.4	30.5	31.6	32.8	33.9	35.0	36.1	37.3	38.4
36	17.1	18.1	19.0	20.1	21.1	22.1	23.2	24.2	25.3	26.4	27.5	28.6	29.7	30.8	31.9	33.0	34.1	35.2	36.3	37.4	38.5

Appendix B. Site Index table for second-growth coastal red alder from Mitchell and Polsson (1988), modified from Harrington and Curtis (1986). bh = Breast height. (continued)

bh age (yrs)	Red alder Site Index																				
	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
	Top height (m)																				
37	17.3	18.3	19.3	20.3	21.3	22.4	23.4	24.5	25.5	26.6	27.7	28.8	29.9	31.0	32.1	33.2	34.3	35.4	36.5	37.6	38.7
38	17.6	18.5	19.5	20.6	21.6	22.6	23.7	24.7	25.8	26.9	27.9	29.0	30.1	31.2	32.3	33.4	34.5	35.6	36.7	37.8	38.8
39	17.8	18.8	19.8	20.8	21.8	22.9	23.9	25.0	26.0	27.1	28.2	29.2	30.3	31.4	32.5	33.6	34.7	35.7	36.8	37.9	39.0
40	18.0	19.0	20.0	21.0	22.1	23.1	24.1	25.2	26.2	27.3	28.4	29.4	30.5	31.6	32.7	33.7	34.8	35.9	37.0	38.1	39.1
41	18.2	19.2	20.2	21.3	22.3	23.3	24.4	25.4	26.4	27.5	28.6	29.6	30.7	31.8	32.8	33.9	35.0	36.0	37.1	38.2	39.2
42	18.5	19.5	20.5	21.5	22.5	23.5	24.6	25.6	26.7	27.7	28.8	29.8	30.9	31.9	33.0	34.1	35.1	36.2	37.2	38.3	39.4
43	18.7	19.7	20.7	21.7	22.7	23.7	24.8	25.8	26.8	27.9	28.9	30.0	31.0	32.1	33.2	34.2	35.3	36.3	37.4	38.4	39.5
44	18.9	19.9	20.9	21.9	22.9	23.9	25.0	26.0	27.0	28.1	29.1	30.2	31.2	32.3	33.3	34.3	35.4	36.4	37.5	38.5	39.6
45	19.1	20.1	21.1	22.1	23.1	24.1	25.2	26.2	27.2	28.2	29.3	30.3	31.4	32.4	33.4	34.5	35.5	36.5	37.6	38.6	39.6
46	19.3	20.3	21.3	22.3	23.3	24.3	25.3	26.4	27.4	28.4	29.4	30.5	31.5	32.5	33.6	34.6	35.6	36.6	37.7	38.7	39.7
47	19.5	20.5	21.5	22.5	23.5	24.5	25.5	26.5	27.5	28.6	29.6	30.6	31.6	32.7	33.7	34.7	35.7	36.7	37.8	38.8	39.8
48	19.6	20.7	21.6	22.7	23.7	24.7	25.7	26.7	27.7	28.7	29.7	30.7	31.8	32.8	33.8	34.8	35.8	36.8	37.8	38.9	39.9
49	19.8	20.8	21.8	22.8	23.8	24.8	25.8	26.9	27.9	28.9	29.9	30.9	31.9	32.9	33.9	34.9	35.9	36.9	37.9	38.9	39.9

Appendix B. Site Index table for second-growth coastal red alder from Mitchell and Polsson (1988), modified from Harrington and Curtis (1986). bh = Breast height. (continued)

bh age (yrs)	Red alder Site Index																				
	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
	Top height (m)																				
50	20.0	21.0	22.0	23.0	24.0	25.0	26.0	27.0	28.0	29.0	30.0	31.0	32.0	33.0	34.0	35.0	36.0	37.0	38.0	39.0	40.0
51	20.2	21.2	22.2	23.2	24.2	25.1	26.2	27.1	28.1	29.1	30.1	31.1	32.1	33.1	34.1	35.1	36.1	37.1	38.1	39.1	40.1
52	20.3	21.3	22.3	23.3	24.3	25.3	26.3	27.3	28.3	29.3	30.2	31.2	32.2	33.2	34.2	35.2	36.2	37.1	38.1	39.1	40.1
53	20.5	21.5	22.5	23.5	24.5	25.4	26.4	27.4	28.4	29.4	30.4	31.3	32.3	33.3	34.3	35.2	36.2	37.2	38.2	39.2	40.2
54	20.7	21.7	22.6	23.6	24.6	25.6	26.6	27.5	28.5	29.5	30.5	31.4	32.4	33.4	34.3	35.3	36.3	37.3	38.2	39.2	40.2
55	20.8	21.8	22.8	23.8	24.7	25.7	26.7	27.7	28.6	29.6	30.6	31.5	32.5	33.5	34.4	35.4	36.4	37.3	38.3	39.3	40.2
56	21.0	22.0	22.9	23.9	24.9	25.8	26.8	27.8	28.7	29.7	30.7	31.6	32.6	33.5	34.5	35.5	36.4	37.4	38.3	39.3	40.3
57	21.1	22.1	23.1	24.1	25.0	26.0	26.9	27.9	28.9	29.8	30.8	31.7	32.7	33.6	34.6	35.5	36.5	37.4	38.4	39.4	40.3
58	21.2	22.2	23.2	24.2	25.1	26.1	27.1	28.0	29.0	29.9	30.9	31.8	32.7	33.7	34.6	35.6	36.5	37.5	38.4	39.4	40.3
59	21.4	22.4	23.3	24.3	25.3	26.2	27.2	28.1	29.1	30.0	30.9	31.9	32.8	33.8	34.7	35.6	36.6	37.5	38.5	39.4	40.4
60	21.5	22.5	23.5	24.4	25.4	26.3	27.3	28.2	29.1	30.1	31.0	31.9	32.9	33.8	34.7	35.7	36.6	37.6	38.5	39.5	40.4
61	21.7	22.6	23.6	24.6	25.5	26.4	27.4	28.3	29.2	30.2	31.1	32.0	32.9	33.9	34.8	35.7	36.7	37.6	38.5	39.5	40.4
62	21.8	22.8	23.7	24.7	25.6	26.5	27.5	28.4	29.3	30.2	31.2	32.1	33.0	33.9	34.8	35.8	36.7	37.6	38.6	39.5	40.5
63	21.9	22.9	23.8	24.8	25.7	26.6	27.6	28.5	29.4	30.3	31.2	32.1	33.1	34.0	34.9	35.8	36.7	37.7	38.6	39.5	40.5

Appendix B. Site Index table for second-growth coastal red alder from Mitchell and Polsson (1988), modified from Harrington and Curtis (1986). Bh = breast height. (continued)

bh age (yrs)	Red alder Site Index																				
	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
	Top height (m)																				
64	22.0	23.0	23.9	24.9	25.8	26.7	27.7	28.6	29.5	30.4	31.3	32.2	33.1	34.0	34.9	35.9	36.8	37.7	38.6	39.6	40.5
65	22.1	23.1	24.0	25.0	25.9	26.8	27.8	28.7	29.6	30.5	31.4	32.3	33.2	34.1	35.0	35.9	36.8	37.7	38.7	39.6	40.5
66	22.3	23.2	24.2	25.1	26.0	26.9	27.8	28.7	29.6	30.5	31.4	32.3	33.2	34.1	35.0	35.9	36.8	37.7	38.7	39.6	40.5
67	22.4	23.3	24.3	25.2	26.1	27.0	27.9	28.8	29.7	30.6	31.5	32.4	33.3	34.2	35.1	36.0	36.9	37.8	38.7	39.6	40.6
68	22.5	23.4	24.4	25.3	26.2	27.1	28.0	28.9	29.8	30.7	31.5	32.4	33.3	34.2	35.1	36.0	36.9	37.8	38.7	39.7	40.6
69	22.6	23.5	24.5	25.4	26.3	27.2	28.1	29.0	29.8	30.7	31.6	32.5	33.4	34.2	35.1	36.0	36.9	37.8	38.7	39.7	40.6
70	22.7	23.6	24.6	25.5	26.4	27.3	28.1	29.0	29.9	30.8	31.6	32.5	33.4	34.3	35.2	36.0	36.9	37.8	38.8	39.7	40.6
71	22.8	23.7	24.6	25.6	26.4	27.3	28.2	29.1	30.0	30.8	31.7	32.6	33.4	34.3	35.2	36.1	37.0	37.9	38.8	39.7	40.6
72	22.9	23.8	24.7	25.6	26.5	27.4	28.3	29.1	30.0	30.9	31.7	32.6	33.5	34.3	35.2	36.1	37.0	37.9	38.8	39.7	40.6
73	23.0	23.9	24.8	25.7	26.6	27.5	28.4	29.2	30.1	30.9	31.8	32.6	33.5	34.4	35.2	36.1	37.0	37.9	38.8	39.7	40.6
74	23.1	24.0	24.9	25.8	26.7	27.5	28.4	29.3	30.1	31.0	31.8	32.7	33.5	34.4	35.3	36.1	37.0	37.9	38.8	39.7	40.6
75	23.2	24.1	25.0	25.9	26.7	27.6	28.5	29.3	30.2	31.0	31.9	32.7	33.6	34.4	35.3	36.2	37.0	37.9	38.8	39.7	40.7