The Relationship Between Productivities of Salmonids and Forest Stands in Northern California Watersheds

Sharon L. Frazey and Margaret A. Wilzbach

ABSTRACT

Productivities of resident salmonids and upland and riparian forests in 22 small watersheds of coastal northern California were estimated and compared to determine whether: 1) upland site productivity predicted riparian site productivity; 2) either upland or riparian site productivity predicted salmonid productivity; and 3) other parameters explained more of the variance in salmonid productivity. Upland and riparian site productivities were estimated using Site Index values for redwood *(Sequoia sempervirens)* and red alder *(Alnus rubra)*, respectively. Salmonid productivity was indexed by back-calculated length at age 1 of the largest individuals sampled and by total biomass. Upland and riparian site indices were correlated, but neither factor contributed to the best approximating models of salmonid productivity. Total salmonid biomass was best described by a positive relationship with drainage area. Length of dominant fish was best described by a positive relationship with percentage of hardwoods within riparian areas, which may result from nutrient and/or litter subsidies provided by red alder. The inability of forest productivity to predict salmon productivity may reflect insufficient variation in independent variables, limitations of the indices, and the operation of other factors affecting salmonid production. The lack of an apparent 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.

Keywords: forestry-fishery interactions, Site Index, red alder, redwood, resident salmonids

Factors affecting upland forest productivity may also affect the ability of adjoining streams to support salmonid production. 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 (e. g., Fralish 1994, McLaughlin and Downing 2002).

The same features influence the carrying capacity of streams for salmonids. For example, water temperature affects availability of dissolved oxygen and metabolic processes of salmonids, with attendant effects on growth rate, productivity, and length of life cycles (Elliott 1994). It also affects the production of macroinvertebrates that form the salmonid prey base (e.g., Benke 1993, Huryn and Wallace 2000). Physical habitat for salmonids is affected by channel morphology (Fukushima 2001, Hicks and Hall 2003), and 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 (e.g., Romagosa and Robison 2003). Competition, predation, pathogens, and anthropogenic activities also play a strong role in affecting salmonid production (Gibson 1988). Along with suitable habitat, prey availability is likely one of the most important factors controlling salmonid production in streams (e.g., Chapman 1966, Gregory et al. 1987, Richardson 1993). The limited success of numerous attempts to establish relationships between salmonid standing crops and in-stream habitat variables (e.g., Fausch et al. 1988, Inoue and Nakano 2001), 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.

Although measurement of in-stream physical habitat often fails to account for prey availability, which is critical for assessing the productive capacity of a stream, measurement of upland productivity subsumes at least some of the factors affecting food availability, such as solar radiation and nutrient supply. For example, nutrients supplied by parent materials may affect production of both forests and fish. Thus, although it has often been difficult to establish relationships between salmonid production and in-stream habitat, one might expect 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 (e.g., Connolly and Hall 1999, Tschaplinski 1999, Young et al. 1999), the relationship between upland productivity and salmonid productivity in the Pacific Northwest has not been examined. For forest managers, it is important to know whether the productivity of potential upslope harvest areas is directly related to, or unrelated to, the capacity of associated stream reaches to support salmonid fishes. How upslope productivity, which likely influences timber harvest objectives, may be manifested in salmonid growth has the potential to significantly impact timber harvest plans.

Because of the key role that riparian vegetation plays in providing an inflow of organic matter and in influencing trophic pathways in streams (Cummins et al. 1989), riparian condition may be a better predictor of salmonid productivity than upland stand productivity. Upland stand productivity may not be a good predictor of riparian condition, as the structure and dynamics of riparian vegetation is strongly affected by complex interactions among hydrology and local geology (Naiman and Décamps 1997). Lack of correspondence between upland and riparian productivity may be especially marked where the riparian zone is dominated by nitrogen-fixing red alder (*Alnus rubra*), as its growth may be relatively independent of soil nutrients (Binkley et al. 1994).

The objective of this study was to quantify relationships between indices of salmonid productivity and upland and riparian forest productivity in small coastal watersheds of northern California. We asked whether: 1) upland site productivity predicted riparian site productivity; 2) either upland or riparian site productivity predicted salmonid productivity; and 3) other parameters explained more of the variance in salmonid productivity than upland or riparian site productivity.

Methods
Study Area
The relationship of upland productivity, riparian condition, and salmonid productivity was evaluated by analyzing data collected from 25 forest stands and their adjoining streams in coastal watersheds of northern California. Sites were located in small watersheds in the 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 years of record (Freeman et al. 2003). Geology of the sites includes Mesozoic and Paleozoic metamorphic rocks, Mesozoic granitic rock, Mesozoic sedimentary rocks, and serpentinized ultramafic rocks (Harden 2003).

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 irideus*). 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 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 second- and third-order tributaries, with moderate gradients ranging from 2 to 9%, and catchments varying in size from 173 to 2,233 ha (Table 1). Study reach lengths were established using the proportional-distance designation (40 · average stream width), a method adopted by the US Environmental Protection Agency Environmental Monitoring and Assessment Program (EMAP) program and described in Barbour et al. (1999). Reach lengths averaged 125 m 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 estimation of forest stand productivity (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 years) attained by dominant and codominant 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 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 provided by Green Diamond Resource Company, where data 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 five (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 four 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 codominant 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. Upslope edge of the riparian zone was delimited by abrupt changes in gradient and changes in vegetation composition. 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 lookup table from Hanson et al. (2003), modified from Krumland and Wensel (1977). Site Index lookup tables link tree height at present age with tree height at a common base age. Field measurements of Site Index were only weakly correlated with Site Index values 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 data set.
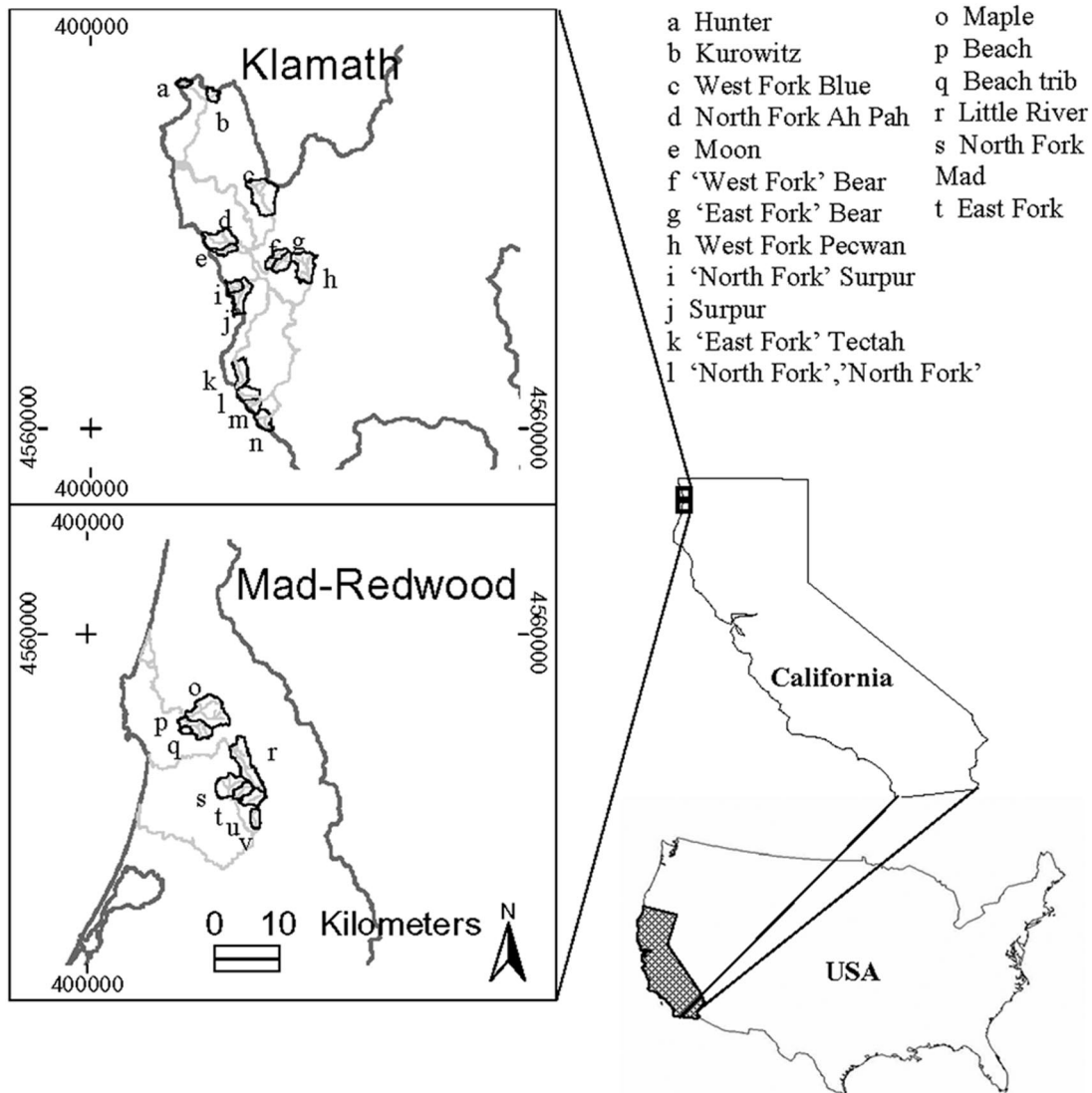
Figure 1. Study sites in the Lower Klamath and Mad-Redwood subwatersheds on the north California coast. Stream reaches surveyed were located at pour points of the corresponding watersheds.

A small proportion of the catchment areas examined (average = 12%) extended beyond lands within Green Diamond Resource Company ownership. These areas had land use similar to 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 (percentage of hardwoods), and percentage of canopy coverage. In five sites, Site Index of redwoods within the riparian area was measured to evaluate the correspondence of redwood Site Index between riparian and upland areas. In March 2003, following leaf-out of riparian hardwoods, measurements of each parameter were made along four evenly spaced transects perpendicular to the stream reach.

Percentage of 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.

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 2 m along transects extending to the edge of the riparian area. Riparian width was determined for each transect by a change in uniform slope and vegetation type. 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 codominant 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. Mean age of bored alder was 30 years (SD = 9, n = 173). Averaged values were used to determine alder Site Index at a base age of 50 years using tables and curves of Mitchell and Polsson (1988).

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	Drainage area (ha)	Upland SI	Riparian SI	Riparian hardwoods	Riparian canopy cover
			(height [ft] at age 50)		(%)	
Beach	Maple Creek	974	121	97	50	89
Beach tributary	Maple Creek	173	121	109	28	90
Canyon	Mad River	723	104	110	53	59
East Fork Bear	Klamath River	603	89	84	64	85
East Fork Mad	Mad River	536	109	109	34	85
East Fork Tectah	Klamath River	775	94	89	52	65
Hunter	Klamath River	224	98	101	74	89
Kurowitz	Klamath River	327	89	103	81	87
Little River	Little River	1817	111	93	54	42
Maple	Maple Creek	2233	117	91	55	93
Moon	Klamath River	371	109	94	83	78
North Fork Ah Pah	Klamath River	1163	114	110	41	90
North Fork Mad	Mad River	1181	116	113	54	68
North Fork Surpur	Klamath River	404	117	106	57	83
North Fork, North Fork Roach	Klamath River	652	106	92	49	80
Pine	Mad River	417	114	100	84	78
South Fork Roach	Klamath River	636	103	88	78	71
South Fork, North Fork Roach	Klamath River	397	102	93	57	85
Surpur	Klamath River	961	115	104	71	83
West Fork Bear	Klamath River	486	101	103	76	87
West Fork Blue	Klamath River	1876	81	85	61	81
West Fork Pecwan	Klamath River	1244	90	81	29	86

Salmonid Productivity

Unlike the Site Index for forest trees, a standardized index of productivity for salmonids has not been established. We chose two metrics: total salmonid biomass (g/m^2), and length at a base age of 1 year among the largest fish sampled. Total biomass of salmonids was chosen as it represents a basic component in the estimation of production that integrates number and size of fish. Previous research has established that salmonid biomass is 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. 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 (e.g., Grant 1990, Nielsen 1992, Keeley 2001), thus supporting the Site Index assumption that growth attained by dominant individuals may be relatively unaffected by density. In common with the unrestrained height growth of site trees, the unrestrained growth in length of dominant fish provides a good index of site potential because it is likely to be relatively stable and robust over a range of fish densities.

Reaches were blocked with 6-mm mesh netting when natural barriers were not present prior to fish sampling. Fish were sampled once from each site during July through August 2002 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 anesthetized with CO_2, identified, measured to the nearest mm fork length, weighed to the nearest 0.01 g, and allowed to recover before being released at the location of capture. Scale samples for analysis of length-at-age were taken from 10 of the largest fish within each reach. Because of an inability to reliably distinguish among juvenile cutthroat, rainbow, and steelhead trout and various hybrids, salmonids were grouped together for analysis.

Table 2. Population density, biomass, and fork length at age 1 of dominant salmonids sampled from the study sites. Fork length was back-calculated from scale analysis and represents the mean from the 10 largest individuals collected at each site.

Creek	Density (no./m^2)	Biomass (g/m^2)	Fork length at age 1 (mm)
Beach	0.63	3.55	108
Beach tributary	0.93	2.73	83
Canyon	2.12	7.75	103
East Fork Bear	0.43	4.49	99
East Fork Mad	0.19	1.91	103
East Fork Tectah	0.30	1.63	109
Hunter	0.54	6.53	105
Kurowitz	0.82	8.75	120
Little River	1.49	11.15	97
Maple	1.48	13.77	99
Moon	0.59	8.34	112
North Fork AhPah	0.46	5.71	104
North Fork Mad	0.14	1.22	97
North Fork Surpur	1.16	8.65	102
North Fork of North Fork Roach	0.89	6.72	89
Pine	0.11	1.63	111
South Fork Roach	0.55	5.99	96
South Fork of North Fork Roach	0.27	3.09	94
Surpur	0.88	11.56	112
West Fork Bear	0.98	5.78	99
West Fork Blue	1.38	15.97	128
West Fork Pecwan	0.13	2.07	98

Salmonid abundance was estimated using the Seber-LeCren (Seber 1982) and the Moran-Zippin (Zippin 1958) estimators for two and more than two passes, respectively. Salmonid density was expressed as no. of fish/m^2. Total biomass (g/m^2) was estimated as mean mass of fish for each size class multiplied by that size class density. Density and biomass of salmonids at each site is given in Table 2.

Fish scales were analyzed using a compound microscope outfitted with a monochrome video camera and digitizing software. A magnification of ×10 was used to capture images. Measurements of
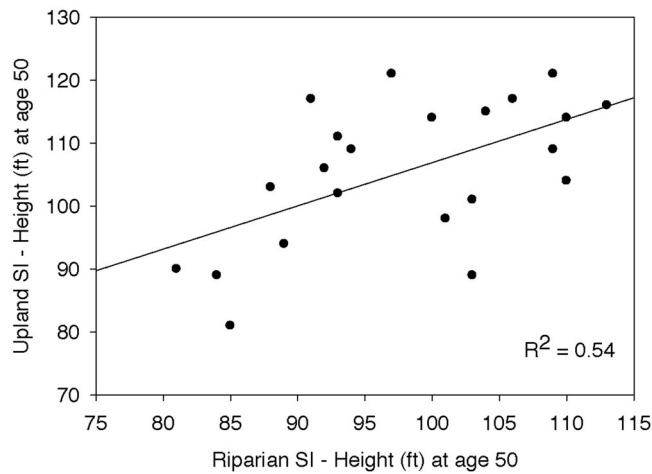
Figure 2. The relationship between Site Index of redwood in upland forest stands and Site Index of red alder in riparian areas.

Figure 3. The relationship between total salmonid biomass and drainage area in 22 watersheds of coastal northern California.

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. Fish length at age 1 was back-calculated using the Fraser-Lee formula (Fraser 1916, Lee 1920).

$$L_i = c + (L_c - c)\left(\frac{S_i}{S_c}\right) \quad (1)$$

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; and c = intercept from the regression of body length on mean scale length. Measurements of the 10 largest individuals were averaged to determine mean length at age 1 among the dominant individuals in each reach. Dominant individuals represented less than 10 percent of the individuals sampled at all sites.

Statistical Analysis

Data were analyzed by constructing linear regression models with total salmonid biomass and length of dominant age 1 salmonids as separate response variables. Drainage area, percentage of 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 (e.g., Kozel and Hubert 1989, Harvey 1998, Roni 2002). 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%). 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.

Candidate models was 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 2 units of the minimum AIC_c value were considered to be valid candidate models. Akaike weights (ω_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.
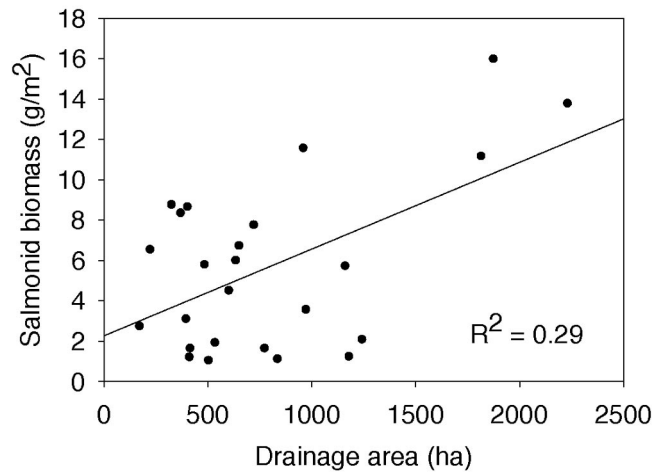
Table 3. Models representing relationships between total salmonid biomass and attributes of upland and riparian forest stands in 22 watersheds in coastal northern California, as measured by AIC_c. Models included all combinations of four independent variables, where 1 = drainage area (positive relationship, +), 2 = upland Site Index (negative relationship, −), 3 = percentage of riparian hardwoods (+), and 4 = riparian Site Index (−). For each model, the coefficient of determination (R^2), differences in AIC_c between models (Δ_i), and Akaike weights (ω_i) are shown. The best-fitting model is highlighted in bold.

Model	R^2	Δ_i	ω_i
1, 2	0.30	10.54	0.00
1, 2, 4	0.30	22.41	0.00
1, 2, 3	0.39	17.80	0.00
1, 4	0.30	10.79	0.00
1, 3, 4	0.39	17.85	0.00
2, 3, 4	0.08	31.62	0.00
1, 2, 3, 4	0.39	30.75	0.00
3, 4	0.07	19.45	0.00
2, 3	0.03	20.74	0.00
4	0.04	9.21	0.01
2	0.00	10.25	0.01
2, 4	0.04	20.40	0.00
1	**0.29**	**0.00**	**0.93**
1, 3	0.39	6.16	0.04
3	0.03	9.53	0.01

Results

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

The best approximating model for total salmonid biomass included a modest positive relationship with drainage area ($R^2 = 0.29$, Figure 3). No other candidate models were within 2 AIC_c units of drainage area (Table 3). The Akaike weight, 0.93, is large relative to the weight of the other models tested, and therefore provides strong evidence in favor of drainage area being the actual best fit model for total biomass of salmonids among the models considered.

A positive relationship with percentage of hardwoods in riparian areas provided the best-approximating model for length of dominant fish at age 1 ($R^2 = 0.30$, Figure 4) with no other models within
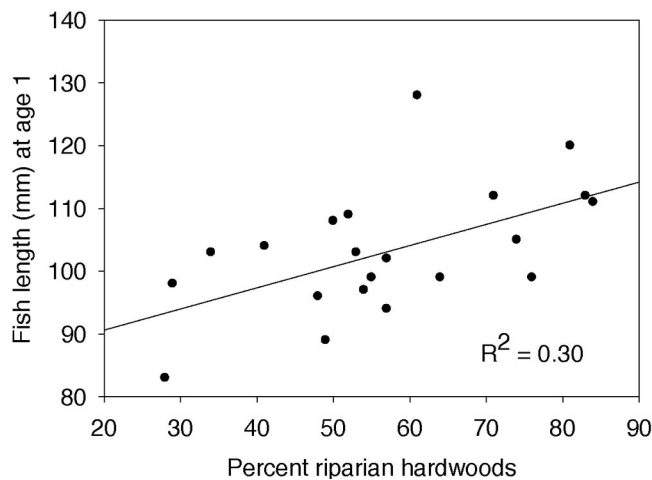
Figure 4. The relationship between fork length of dominant salmonids at age 1 and percentage of riparian hardwoods in 22 watersheds of coastal northern California. Fork length at age 1 was back-calculated from scale analysis, and it represents the mean from the 10 largest individuals collected at each site.

Table 4. Models representing relationships between length of dominant salmonids at age 1 and attributes of upland and riparian forest stands in 22 watersheds in coastal northern California, as measured by AIC_c. Models included all combinations of four independent variables, where 1 = drainage area (positive relationship, +), 2 = upland Site Index (negative relationship, −), 3 = percentage of riparian hardwoods (+), and 4 = riparian Site Index (−). For each model, the coefficient of determination (R^2), differences in AIC_c between models (Δ_i), and Akaike weights (ω_i) are shown. The best-fitting model is highlighted in bold.

Model	R^2	Δ_I	ω_i
1, 2	0.19	18.34	0.00
1, 2, 4	0.26	31.72	0.00
1, 2, 3	0.47	21.52	0.00
1, 4	0.03	23.52	0.00
1, 3, 4	0.38	26.32	0.00
2, 3, 4	0.41	24.69	0.00
1, 2, 3, 4	0.53	34.97	0.00
3, 4	0.30	13.91	0.00
2, 3	0.40	9.84	0.01
4	0.01	9.38	0.01
2	0.16	4.75	0.08
2, 4	0.20	18.01	0.00
1	0.03	8.86	0.01
1, 3	0.38	10.63	0.00
3	**0.30**	**0.00**	**0.89**

2 AIC_c units (Table 4). The Akaike weight of 0.89 provides strong evidence that the percentage of hardwoods model is likely the best. Length of dominant fish was positively correlated with total salmonid biomass from the study sites ($R^2 = 0.42$, Table 2).

Discussion

In this study, Site Indexes of upland redwood and riparian red alder were moderately correlated, but neither Site Index predicted measures of salmonid productivity. The correlation of Site Index between upland and riparian areas likely reflects generally similar environmental requirements of red alder and redwood. That the correlation was not stronger may reflect both 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 the measurements used to estimate productivities of both trees and fish, or 3) the operation of other factors limiting salmonid production that are not encompassed in measures of forest productivity.

Despite efforts to select stream reaches in coastal northern California that exhibited a large range in upland Site Index, most of the selected watershed areas averaged to Site Class II and III (coefficients of variation for upland and riparian Site Index were 11 and 9%, respectively), as lower-quality sites had sparse or absent salmonid populations, and higher-quality sites were located in larger rivers that support anadromous salmonids. Among the land holdings of Green Diamond Resource Company in northern California, more than 80% are classified as Site Class II and III (Gary Warinner, personal communication, Green Diamond Resource Company, Mar. 15, 2006). 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 rather than the latitudinal boundaries of investigation because of the diminishing coastal influence and greater range of climatic and geological conditions as one moves inland.

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 (Stearns-Smith 2001). However, selection of site trees that do not accurately reflect site potential and measurement error may result in spurious conclusions about site productivity (Harrington and Curtis 1986). In common with the Site Index, use of length of dominant fish as a measure of salmonid productivity is subject to error in selection and measurement of dominant individuals, and dependence of growth on conditions during the temporal period of measurement may produce spurious conclusions. 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 (e.g., in the case of small numbers of large individuals), nor does small biomass necessarily result from low productivity.

Failure of either riparian or upland Site Index to predict salmonid productivity may also reflect the operation of factors limiting salmonid production that are not adequately encompassed in measures of forest productivity. For example, temperature regime and the amount of available solar radiation are factors likely affecting the productivity of both salmonid populations (Bisson and Bilby 1998)

and upslope vegetation (Stearns-Smith 2001). But the incorporation of these factors 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 (Naiman and Décamps 1997, Poole and Berman 2001).

Although neither measure 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 (e.g., Harvey 1998), but the explanation for the pattern is not clear. Fish are likely not responding to drainage area per se, but rather to discharge and/or resource supply. Increased discharge would provide greater depth and velocity and flux of food in these small streams with dry summers. Longitudinal gradients in temperature, which affect both fish bioenergetics and secondary production, may also contribute to increases in salmonid production with drainage area.

In our study, salmonid productivity was modestly correlated with the percentage of hardwoods in riparian areas. Red alder was the dominant riparian hardwood tree, so one explanation for the correlation of salmonid productivity with percentage of hardwoods may lie in the increased provisioning of nitrogen to stream reaches as a consequence of nitrogen fixation by alder. Compton et al. (2003) observed strong correlations between the percentage of alder within a watershed and surface water concentrations of nitrate in coastal Oregon. 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 explanation for an increase in fish growth with an increase in the percentage of riparian hardwoods (alder) may lie 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 (e.g., Cummins et al. 1989, Cummins 2002), and it may support a greater biomass of invertebrate prey. Provisioning of nutrients and litter inputs are not mutually exclusive explanations that might account for the relationship between percentage of riparian hardwoods and salmonid growth. Salmonid growth appears to derive largely from autotrophic pathways during spring and summer periods of active growth (Bisson and Bilby 1998), but body mass may be maintained during the winter from heterotrophic pathways. Volk (2004) found increased production of algal and invertebrate communities, and higher levels of specific essential fatty acids in trout, in alder than in conifer dominated streams in the Olympic Peninsula, supporting the possibility that nutrient and/or litter subsidies from red alder underlie a positive correlation between salmonid growth and percentage of riparian hardwoods. Piccolo and Wipfli (2002) also found a greater export of invertebrates to downstream reaches from young growth alder sites than from young growth conifer sites in southeast Alaska.

Upslope production of conifers is the primary focus of commercial harvest interest. Because our study found no evidence of a linkage between upslope conifer productivity and salmonid productivity, an implication is that the management of land for timber productivity and component streams for salmonid production in these sites will require separate, albeit integrated, management strategies. Thus, although timber harvest beyond the riparian likely has general consequences for salmonid production (for example, through sedimentation or recruitment of large woody debris), whether the harvest is of trees from good-quality or poor-quality sites may have little direct consequence for salmonid populations in the streams that flow through these sites.

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