ECOGRAPHY 28: 537–551, 2005

Influences of the vegetation mosaic on riparian and stream environments in a mixed forest-grassland landscape in "Mediterranean" northwestern California

Hartwell H. Welsh, Jr, Garth R. Hodgson and Nancy E. Karraker

Welsh, H. H. Jr, Hodgson, G. R. and Karraker, N. E. 2005. Influences of the vegetation mosaic on riparian and stream environments in a mixed forest-grassland landscape in "Mediterranean" northwestern California. – Ecography 28: 537–551.

We examined differences in riparian and aquatic environments within the three dominant vegetation patch types of the Mattole River watershed, a 789-km^2 mixed conifer-deciduous (hardwood) forest and grassland-dominated landscape in northwestern California, USA. Riparian and aquatic environments, and particularly microclimates therein, influence the distributions of many vertebrate species, particularly the physiologically-restricted ectotherms – reptiles and amphibians (herpetofauna), and fishes. In addition to being a significant portion of the native biodiversity of a landscape, the presence and relative numbers of these more tractable small vertebrates can serve as useful metrics of its "ecological health." Our primary objective was to determine the range of available riparian and aquatic microclimatic regimes, and discern how these regimes relate to the dominant vegetations that comprise the landscape mosaic. A second objective, reported in a companion paper, was to examine relationships between available microclimatic regimes and herpetofaunal distributions. Here we examined differences in the composition, structure, and related environmental attributes of the three dominant vegetation types, both adjacent to and within the riparian corridors along 49 tributaries. Using automated dataloggers, we recorded hourly water and air temperatures and relative humidity throughout the summer at a representative subset of streams; providing us with daily means and amplitudes for these variables within riparian environments during the hottest period. Although the three vegetation types that dominate this landscape each had unique structural attributes, the overlap in plant species composition indicates that they represent a seral continuum. None-the-less, we found distinct microclimates in each type. Only riparian within late-seral forests contained summer water temperatures that could support cold-water-adapted species. We evaluated landscape-level variables to determine the best predictors of water temperature as represented by the maximum weekly maximum temperature (MWMT). The best model for predicting MWMT (adj. $R^2 = 0.69$) consisted of catchment area, aspect, and the proportion of non-forested (grassland) patches. Our model provides a useful tool for management of cold-water fauna (e.g. salmonids, stream amphibians) throughout California's "Mediterranean" climate zone.

H. H. Welsh Jr (hwelsh@fs.fed.us), G. R. Hodgson and N. E. Karraker, U.S. Forest Service, Pacific Southwest Research Station, Redwood Sciences Lab., 1700 Bayview Dr., Arcata, CA 95521, USA (present address of N. E. K.: Environmental Science and Forestry, State Univ., of New York, Syracuse, 1 Forestry Dr., Syracuse, NY 13210, USA).

Accepted 17 March 2005

ISSN 0906-7590

Essential to determining what fauna can be supported by a landscape are the plant assemblages, their successional stages, related structural attributes, and the relative amounts and spatial configurations of these assemblages across the landscape mosaic (Wiens 1996). Aquatic and riparian environments greatly expand the range of available microclimates within a landscape (Naiman et al. 1998, Chen et al. 1999), and generally support the highest biodiversity (Naiman et al. 1993, Ward 1998). This enhanced biodiversity results because these environments support many species that are uniquely adapted to conditions found only in cooler, moister riparian and aquatic habitats (e.g. fishes, amphibians, aquatic-adapted reptiles like turtles and water snakes, and aquatic- and riparian-adapted birds and mammals). Areas of suitable microclimates are of particular importance in determining where ectothermic vertebrates (reptiles, amphibians, fishes) can exist, because these organisms have limited physiological abilities to control body temperature (Elliott 1981, Dunham et al. 1989, Huey 1991). In northwestern California, where warmer "Mediterranean" and cooler Pacific Northwest climatic regimes meet, riparian and aquatic environments are critical to sustaining many native anadromous species (Moyle and Yoshiyama 1994, Stouder et al. 1997). Consequently, science-based management of aquatic and riparian areas is critical to maintaining the viability of many commercially important species, and the relatively high native biodiversity of these landscapes. Of particular interest for informed management is knowledge of how upland processes and activities such as plant community succession, fire, and timber harvesting, influence riparian and aquatic environments and their ability to sustain resident biota (Gregory 1997, Perry and Amaranthus 1997, Welsh et al. 2000).

Here we examine the relationships between the major vegetation mosaic elements in a northwestern California watershed, the internal structures of those elements, and the influence of these structures on conditions within riparian environments. Our primary objective was to examine the influence of vegetation composition and related seral stage on the available fine-scale environments within patch types, particularly the riparian and aquatic environments and associated microclimates, across this landscape. We considered an analysis based on seral stage differences to be a reasonable surrogate for one which would follow site conditions through time as succession progresses. Succession in this region influences, and is influenced by, both natural and anthropogenic events such as fire and timber harvesting that characterize the local disturbance regime.

In this paper we present our analysis of the landscape mosaic and its internal characteristics as they relate to particular requirements of the native vertebrate ectotherms. We then sought to correlate this information with faunal distribution patterns (herpetofauna; see companion paper [Welsh et al. 2005]; and fish [Welsh et al. 2001]), in an attempt to understand the linkages between vegetation mosaic patches, microclimatic regimes, faunal distribution patterns, and processes operating at the scale of the greater landscape. Based on the linkages between mosaic patch conditions and animal patterns that we have uncovered, we offer a practical application of our resulting ability to model unique habitat conditions on this landscape. We present a model for stream temperature, based on landscape-scale attributes, that predicts the ability of a given catchment to support cold-water-adapted species, and in particular the threatened coho salmon.

Study area

The Mattole watershed (hereafter the Mattole) lies in the North Coast Bioregion of California (Welsh 1994) in Humboldt and Mendocino counties (Fig. 1). The Mattole covers 789 km^2, lying mostly east of the King Range Mountains (King Peak = 1318 m), which shields it from climatic influences of the Pacific Ocean, and

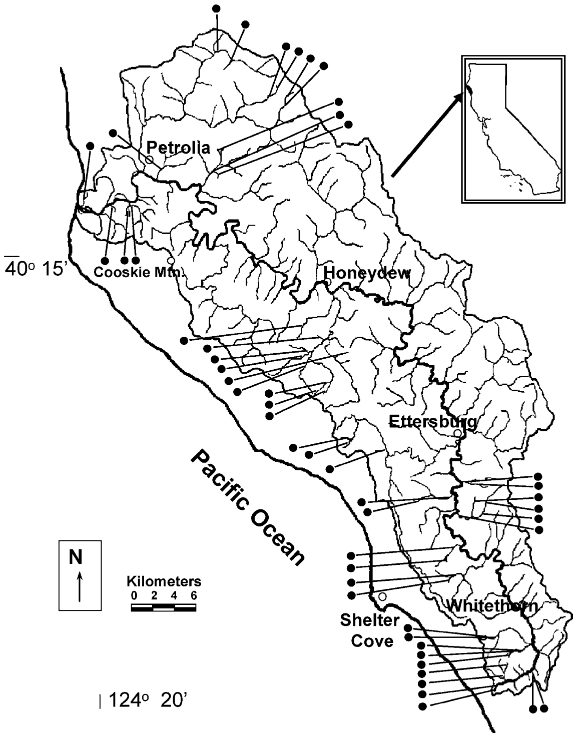

Fig. 1. Location of the Mattole watershed (between 39°57′ and 40°25′ latitude and 123°52′ and 124°21′ longitude) in northwestern California, USA. Closed circles indicate locations of the 49 stream reaches sampled from 1994 to 1996.

creates a Mediterranean-like climate of hot, dry summers and mild, wet winters typical of the interior coast ranges of northwestern California. Only the mouth of the Mattole in the north, and the headwaters area at the south end of the watershed (Fig. 1), experience the influence of cooling marine fog in the summer. Common plant associations within the Mattole include: 1) mixed redwood *Sequoia sempervirens* and Douglas-fir *Pseudotsuga menziesii* forest (restricted to areas of the Mattole headwaters); 2) mixed Douglas-fir and deciduous or hardwood (primarily tanoak *Lithocarpus densiflora* and madrone *Arbutus menziesii*) forest; 3) mixed chaparral consisting primarily of manzanita *Arctostaphylos* spp., mountain whitethorn *Ceanothus cordulatus*, scrub oak *Quercus berberidifolia*, and coyote brush *Baccharis pilularis*; and 4) grasslands (104 km^2). Mixed Douglas-fir/hardwood forest dominates most of the watershed, with a range of seral stages from young (from recent fires and logging) (506 km^2) to old-growth forests (50 km^2). The chaparral (98 km^2) is patchy and found mostly at higher elevations along the western margin of the watershed, rarely adjacent to riparian areas. In addition to the above species, riparian areas of the Mattole also contain bigleaf maple *Acer macrophyllum*, red alder *Alnus rubra*, cottonwood *Populus fremontii*, Oregon ash *Fraxinus latifolia*, and willow *Salix* spp.

Materials and methods

Because our primary interest was to examine the range of riparian and aquatic conditions in this watershed as they relate to landscape-scale parameters, and particularly the vegetation mosaic, we sought to find a set of representative sub-watersheds that were wholly or mostly covered by each of the most common vegetation assemblages, and that were located on accessible federal or private lands. We first used aerial photographs and ground reconnaissance to examine the structure and floristic composition of dominant plant assemblages across the watershed. This reconnaissance indicated that three distinct, relatively homogeneous vegetative assemblages dominate this landscape: 1) open grassland, often including small patches of second-growth Douglas-fir/mixed hardwood forest (hereafter mixed grassland), 2) homogeneous second-growth Douglas-fir/mixed hardwood forest, and 3) late-seral Douglas-fir/mixed hardwood forest. The latter is far less common than the other two types (Fig. 2). Each of these three vegetation types varies somewhat in plant species composition, particularly in the relative amounts of conifers versus hardwood species, depending upon slope, aspect, elevation, and soil characteristics. However, each is readily identifiable remotely as a distinct physiognomic type on the landscape, and these unique patches

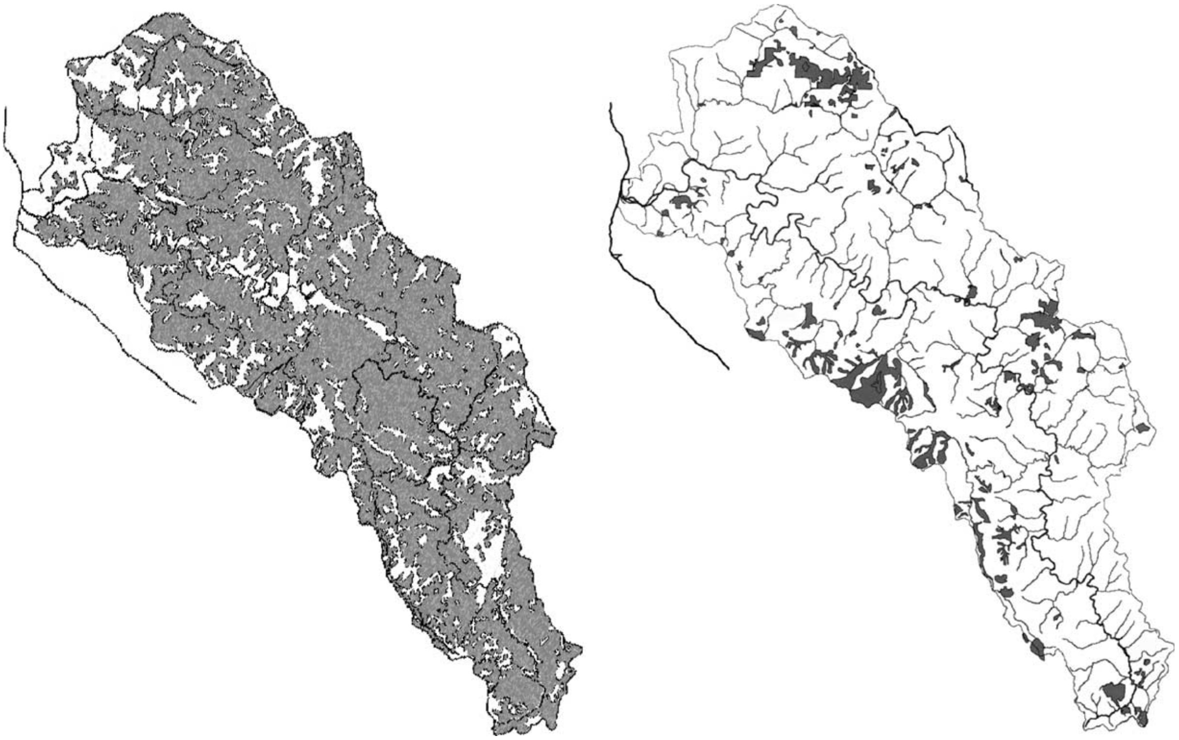

Fig. 2. Comparison of late-seral environments (dark tones) in the Mattole watershed in 1947 and 1997. Maps were originally derived from aerial photographs. Modified from Mattole Restoration Council maps issued in 1988 and 1997.

provided a convenient framework both to distribute our stream sampling reaches systematically across the range of available riparian/aquatic environments, and to later examine structural and microclimatic differences within these vegetations. Rarely did one of the three vegetation types cover an entire sub-watershed, rather most sub-watersheds contained two or more types, but usually with one type being dominant such that we could characterize each reach by dominant vegetation type. While the systematic distribution of study reaches within the Mattole was somewhat hindered by access restrictions, the watershed contains sufficient federal lands (U.S. Bureau of Land Management), and co-operative landowners, that we were able to sample nearly the full range of streamside and aquatic environments at sites well-distributed throughout the watershed (Fig. 1). Our second objective was to evaluate differences in herpetofaunal composition both between vegetation types and between perennial and intermittent streams (see companion paper, Welsh et al. 2005), so where possible we selected both a perennial and intermittent reach in each sub-watershed. This design resulted in a sample of 49 stream reaches distributed in 31 tributary drainages of the Mattole (Fig. 1); stream order for these reaches ranged from first to third.

Each sample stream reach was a randomly selected, 300 m length of perennial or intermittent stream situated entirely within one of the three vegetation types. We sampled stand vegetation and other environmental features in 1/10th and 1/5th ha circular plots (see below) centered at mid-reach, coincident with our animal sampling (details in Welsh et al. 2005). These data were used initially to verify the vegetation classification of each sample reach, and to correct any questionable assignments prior to analysis of animal relationships. They were then used in a discriminant function analysis (DA) to ascertain the distinguishing environmental features within patches of each of the three primary vegetation types (see below). Lastly, these data were used to identify and model key environmental features associated with herpetofauna detected (reported in Welsh et al. 2005).

Multi-scale measurements of environmental variables

Because this study incorporates a range of spatial scales, landscape, macro-environment, meso-environment, and micro-environment, we here define our terms more precisely from the coarsest to the finest level of resolution (note these categories are not mutually exclusive).

The landscape-scale

This scale is relevant for evaluation of biotic and abiotic patterns expressed across the range of available topographic features, including vegetation mosaic elements, with variation expressed at the level of sub-basin and greater (we sampled sub-basins ranging in size from 22 to 9775 ha). Features depicted at this scale included such attributes as the relative amounts of the primary vegetation assemblages, macro-climatic variables such as annual minimum and maximum air temperatures and solar illumination (all described below), and other major landscape features such as catchment aspect and elevation. Estimated values for these landscape-scale attributes were determined in a GIS environment using ArcView software.

The macro-environment scale

This scale pertained to variables describing the structure and plant species composition of individual landscape mosaic patches, such as forest stands or meadow expanses, with relatively homogeneous plant assemblages. Variables depicted at this scale of resolution include measures of the physiognomy of forest stands (e.g. tree composition by size class, ground cover vegetation), which we used to characterize the environment surrounding each riparian stream reach. We used 35 variables to characterize vegetation seral stage, stand structure, and species composition at each site. These variables were collected in 0.1 or 0.2 ha circles centered on the 300-m stream reach, and from two 10 m long × 0.1 m wide line transects placed on the upslope edges of the 0.1 ha circle and parallel to the stream channel (see Table 1 for the 35 macro-environmental variables).

The meso-environment scale

This scale consisted of variables depicting conditions within the riparian vegetation and stream channel areas surrounding and immediately adjacent to the 300-m wetted channels of our stream reaches. This level of resolution pertains to such variables as stream width, aspect, and the gradient of stream habitat units (run, riffle, pool), over-stream canopy closure, and streambed substrate composition. We used 33 meso-environmental variables to characterize the riparian zone and stream channel conditions along each reach. These variables included conditions in the riparian zone particularly relevant to ectothermic vertebrates (e.g. solar index, water temperature, percent canopy closure; see Magnuson et al. 1979, Huey 1982, Hutchison and Dupre 1992). Meso-environmental data were collected from three 10 × 1 m line transects crossing the stream channel at the top, middle, and bottom of a 0.1 ha circle centered on each reach, and from six animal sample units placed randomly along each reach (see Welsh et al. 2005) (see Table 2 for the 33 meso-environmental variables).

The micro-environment scale

This scale consisted of attributes observed within close proximity to the captures of particular animals that were

Table 1. Results of discriminant analyses of 35 macro-environmental attributes. These variables were sub-set into seven ecological components, each analyzed separately. P to enter and remove was set at 0.10. Canonical variates (CV) are reported only for those with $p \leq 0.10$. Models with heterogeneous variance-covariance matrices are indicated with an asterisk (*). Means and standard deviations are for untransformed data. Variables listed below test results were included in the analyses but did not enter the models. C = Count variable (numbers per ha); T = Line transect variable (percent of 20 m line transect). † = Variable transformed for statistical analysis.

	Vegetation cover type							
Variables	Mixed grassland n = 12		Late seral n = 21		Second growth n = 16		Standardized structure coefficient	
	Mean	SD	Mean	SD	Mean	SD	CV1	CV2
*Geographic relationships								
Elevation (m)	658.3	381.14	1595	659.20	1029	393.83	0.94	−0.33
Aspect (°)	212.42	57.02	216.86	118.02	136.06	121.38	0.25	0.97
	Wilks' λ = 0.546; F (DF = 4, 90) = 7.948; p = 0.0001							
Slope (%)								
†Drainage area (ha)								
*Trees: count by size[1] or status								
†Stumps_C	2.05	1.94	0.26	0.83	2.89	1.82	−0.79	
Large conifers_C	9.58	13.39	45.71	31.71	13.13	22.05	0.68	
Small conifers_C	86.67	100.21	73.33	113.46	200.00	113.49	−0.50	
†Small hardwoods_C	18.68	7.67	21.76	9.20	19.32	6.51	0.20	
	Wilks' λ = 0.339; F (DF = 8, 86) = 7.704; p = 0.0001							
†Large hardwoods_C								
†Snags_C								
Bole_T								
Ground level vegetation								
†Grass_T	2.68	1.81	0.54	0.97	1.00	1.38	0.73	
†Moss_T	1.67	0.94	2.63	0.77	1.65	1.37	−0.56	
†Herb_T	2.54	1.10	1.23	1.05	1.90	1.40	0.60	
	Wilks' λ = 0.470; F (DF = 6, 88) = 6.720; p = 0.0001							
†Ferns_T								
*Dead and down wood[2]								
†Large conifer logs_C	2.60	2.57	4.41	0.85	3.94	1.47	0.79	0.61
†Large hardwood logs_C	2.75	2.05	2.23	1.90	1.02	1.59	−0.57	0.82
	Wilks' λ = 0.707; F (DF = 4, 90) = 4.259; p = 0.0033							
†Log_T								
†Small conifer logs_C								
†Small hardwood logs_C								
†Sound conifer logs_C[3]								
†Sound hardwood logs_C[3]								
Ground cover								
†Lichen litter_T	0.04	0.09	0.12	0.10	0.02	0.05	0.78	
†Rock_T	1.06	1.12	1.40	1.26	0.63	1.34	0.40	
†Exposed soil_T	1.80	1.42	0.97	1.17	1.84	1.37	−0.52	
	Wilks' λ = 0.623; F (DF = 6, 88) = 3.915; p = 0.0016							
Leaf litter_T								
Litter depth_T								
Shrub and understory composition								
†Understory conifer_T[4]	1.49	1.51	1.04	1.30	2.08	1.34	1.0	
	Wilks' λ = 0.897; F (DF = 2, 46) = 2.628; p = 0.0830							
Understory hardwood_T								
Large shrubs_T								
Small shrubs _T								
*Forest climate								
†% canopy closed	3.98	0.95	4.57	0.10	4.51	0.16	0.74	
Surface soil temp. (°C)	20.70	3.97	16.69	2.98	17.72	3.58	−0.70	
Solar index	1.58	1.16	2.91	1.30	2.25	1.13	0.64	
	Wilks' λ = 0.602; F (DF = 6, 88) = 4.235; p = 0.0009							
10 cm depth soil temp. (°C)								

---

[1] Small trees (1/10 ha circle) = classes 1 (12–26.9 cm DBH [diameter at breast height]) and 2 (27–52.9 cm DBH); large trees (1/5 ha circle) = classes 3 (53–89.9 cm DBH), 4 (90–119.9 cm DBH), and 5 (120+ cm DBH).

[2] Data collected in 1/10 ha circle. Small and large hardwood and conifer variables include both sound and decayed log decay status. Refer to footnote 1 for size classes.

[3] "Sound" category encompasses DBH classes 1–5.

[4] "Understory" indicates trees <12 cm DBH (diameter at breast height).

[5] Solar index is an estimate of annual incident solar radiation based on latitude, slope and aspect (Frank and Lee 1966).

Table 2. Results of discriminant analyses of 33 meso-environmental attributes. These variables were sub-set into seven ecological components, each analyzed separately. P to enter and remove was set at 0.10. Canonical variates (CV) are reported only for those with p ≤0.10. Models with heterogeneous variance-covariance matrices are indicated with an asterisk (*). Means and standard deviations are from untransformed data. Variables listed below test results were included in the analyses but did not enter the models. T = Line transect variable (percent of 20 m line transect). † = Variable transformed for statistical analysis.

Variables	Vegetation cover type							
	Mixed grassland n = 12		Late seral n = 21		Second growth n = 16		Standardized structure coefficient	
	Mean	SD	Mean	SD	Mean	SD	CV1	CV2
Riparian climate[1]								
Stream temperature (°C)	15.97	2.55	12.74	1.69	13.54	2.17	1.00	
	Wilks' λ = 0.705; F (DF = 2, 45) = 9.410; p = 0.0004							
†% stream canopy closed								
†% riparian canopy closed								
Surface soil temp. (°C)								
10 cm depth soil temp. (°C)								
*Ground vegetation								
†Herbs_T	2.55	0.53	1.38	0.75	2.41	1.03	0.54	−0.88
†Grass_T	2.43	1.24	0.49	0.75	0.99	1.14	0.72	0.74
	Wilks' λ = 0.485; F (DF = 4, 90) = 9.802; p = 0.0001							
Moss_T								
†Lichen_T								
†Ferns_T								
Ground cover								
†Exposed soil_T	2.52	1.02	0.83	1.00	2.46	0.96	1.00	
	Wilks' λ = 0.579; F (DF = 2, 46) = 16.726; p = 0.0001							
Litter depth (cm)								
Leaf litter_T								
Live and dead wood								
†Large shrubs_T	0.76	1.24	1.97	1.51	1.09	1.31	1.00	
	Wilks' λ = 0.869; F (DF = 2, 46) = 3.471; p = 0.0395							
†Understory conifer_T[2]								
†Understory hardwood_T								
†Logs_T								
†Bole_T								
Small shrubs_T								
*Fine substrates (%)								
†Fines	2.40	0.47	1.48	0.98	2.26	0.98	1.00	
	Wilks' λ = 0.806; F (DF = 2, 46) = 5.527; p = 0.0071							
Sand								
Gravel								
†Organic								
Embedded								
*Coarse substrates (%)								
Boulder	17.28	12.67	26.97	16.24	11.49	8.44	1.00	
	Wilks' λ = 0.782; F (DF = 2, 46) = 6.404; p = 0.0035							
Pebble								
Cobble								
†Bedrock								
Channel attributes								
†Habitat length (m)								
†Channel width (m)								
†Slope (%)								
Mean depth (cm)								
Maximum depth (cm)								

[1] For riparian climate ecological component, second-growth landscape cover type, n = 15, due to lack of data for one stream.

[2] Small trees (1/10 ha circle) = classes 1 (12–26.9 cm DBH [diameter at breast height]) and 2 (27–52.9 cm DBH); large trees (1/5 ha circle) = classes 3 (53–89.9 cm DBH), 4 (90–119.9 cm DBH), and 5 (120+ cm DBH).

the focus of the companion study (Welsh et al. 2005), including water and air temperature at the location of capture. In this paper, the only micro-environmental data we report are those describing available summer micro-climatic variability within and adjacent to the stream reaches which were sampled hourly with automated dataloggers. At a randomly selected subset of four stream reaches within each of the three vegetation types described above we established automated datalogger stations. These stations constantly monitored, and recorded at 1-h intervals, water temperature (one per stream – placed at the lower end of the reach in a deep pool with mixing water at the pool bottom), riparian air temperature, and relative humidity (seven per stream). Air temperature and relative humidity dataloggers were set at 2 cm above ground under insulated covers and placed at set distances with one at streamside (<1 m from the wetted channel) and one each at 10, 20, and 30 m, from the channel edge on each side of twelve representative perennial streams (4 in each primary vegetation type). The microclimate data for each of the three vegetation types were averaged for the same summer time periods at each comparable datalogger station (one water, seven air and two relative humidity) for each of the four representative sites within each of the vegetation types. We evaluated summer maximum temperatures because greater daily extremes occur during the summer and are more limiting to cool temperate-adapted fauna at this latitude than would be winter minimums (see Magnuson et al. 1979, Dunham et al. 1989, Huey 1991).

Predicting water temperature regimes at the landscape scale

Our analysis of environmental variability at the macro- and meso-scales along the 49 stream reaches revealed a significant association between primary vegetation type and stream temperature (results below). However, upstream catchment conditions, compared with those of adjacent upslope and at streamside, can have an overriding influence on stream temperatures (Poole and Berman 2001). In order to examine the influence of upstream catchment conditions on stream temperature regimes we augmented our dataset by combining our stream temperature data from a subset of 9 representative reaches (only 9 of the 12 had complete water temperature data for the entire period of interest) with comparable data from 31 additional Mattole tributaries where personnel from the Mattole Salmon Group (a group of local citizens working to enhance the native fisheries) had obtained additional stream temperature data using our protocol. This resulted in a set of 40 tributaries where continuous water temperature data were collected over the warmest part of each year (August), with data available for at least one, and up to eight years, for each of these streams (1995–2002) (sample $=40$ individual streams with a total dataset comprised of 115 water temperature profiles for August). In all cases these water temperatures were measured hourly in a deep mixing pool at the catchment outlet throughout the entire summer. We used these hourly stream temperature data to calculate the mean maximum stream temperature for the warmest 7-d period of the summer (defined as the maximum weekly maximum temperature or MWMT), the period when cold-water-adapted fauna would experience the greatest stress (for discussion see Welsh et al. 2001).

For each of these 40 tributaries we determined catchment size (ha^2) above the water temperature monitoring site and the relative amounts of forest cover and grassland or open areas that comprised the vegetation mosaic of each catchment. For this analysis we had to combine late-seral and second-growth forest into a single category of “forested habitat” because the late-seral was too scarce (see Fig. 2) to evaluate its present influences at the landscape scale. To evaluate the distribution of vegetation types by sub-watershed we used U.S. Geological Services (USGS) 1992 digital orthophoto quadrangles (DOQ’s) in a GIS environment (ArcView) to delineate polygons with a minimal mapping unit of 0.25 ha. In areas for which DOQ’s were not available ($<10\%$) we defined vegetation polygons using data derived from Landsat Imagery from the U.S. Fish and Wildlife Service, Klamath Bioregional Assessment Project (KBAP). Using GIS, we also determined values for the following landscape-level variables for each catchment: mean elevation; aspect (of the tributary channel); maximum (21 June) illumination (using the ArcView function “Hillslope” that determines the hypothetical solar illumination [time and intensity] of a particular location on a given day, which also takes into account hill slope shading); and the average maximum and minimum air temperatures for August (the month when stream temperatures in the Mattole reached their maximums). Mean air temperatures were determined using data available for the thirty-year time period from 1961 to 1990, at a 2 km^2 resolution, based on Parameter-elevation Regressions on Independent Slopes Models (hereafter PRISM: Daly et al. 1994). Finally, in order to account for two additional sources of variability in stream temperatures, we included “distance from coast” (to account for the potential ameliorating effects of the Pacific Ocean), and an air temperature MWMT calculated from air temperatures during the hottest week of August of each year in the dataset (1995–2002). The “distance to coast” variable was measured based on straight-line distance measured (in meters) in GIS between the site of the datalogger installation in each catchment and the nearest point on the coast. The yearly August air MWMTs were calculated using data from Cooskie Mountain (a weather station on the north-western rim of the Mattole watershed (Fig. 1). The intent was to use the air temperature MWMTs to represent annual variation in this parameter which is thought to be one of the primary natural drivers of stream temperatures (Poole and Berman 2001). In the case of the air MWMT, the only independent variable that might change between years, we added values for each of the eight years for which we had continuous water temperature data (water MWMTs) for the month of August for any sub-basin. The yearly August air MWMT was modeled as a fixed effect. We then used these variables, both alone and in all possible combinations, to construct a set of competing models, testing their relative ability to predict tributary stream temperature as expressed by MWMT.

Statistical analyses

Environmental variables

The 35 macro-environmental variables (Table 1) from 49 reaches were used to describe and differentiate the macro-environment within the three air photo or ground reconnaissance-defined vegetation assemblage types (mixed grassland, second-growth, and late-seral forest), and to re-assign several mis-classified reaches before analysis of animal relationships (reported in Welsh et al. 2005). The 33 meso-environmental variables (Table 2) were used to determine those variables that best distinguished riparian zone and channel conditions among the three vegetation types. We conducted preliminary descriptive analyses to assess normality of all variables, and corrected deviations with appropriate transformations (Sokal and Rohlf 1981). For multivariate analyses, we assumed that univariate normality implied multivariate normality but did not directly test for multivariate normality.

Prior to analysis, the two sets of environmental variables were divided into subsets that represent ecologically meaningful classes of structural, compositional, or climatic attributes of the forest or stream environment (Tables 1 and 2; approach discussed in Welsh and Lind 1995). A three-group discriminant analysis (DA) (Anon. 1990) was performed on each ecological subset (Tables 1 and 2), using a stepwise procedure to select variables. In each case we tested the research hypothesis that there were differences between the three vegetation types for a given variable or set thereof. For model-building, a variable was entered if its p value for the partial F statistic was ≤ 0.10. For final model acceptance and subsequent testing, we also set $\alpha \leq 0.10$. This moderate α-level reduces the chance of type II errors and is more appropriate for detecting ecological trends (Toft 1991, Schrader-Frechette and McCoy 1993). A linear or quadratic discriminant function was then calculated based on the variables selected. We used Bartlett's modification of the likelihood ratio test to test the homogeneity of variance-covariance matrices (Anon. 1990).

We then combined all resulting significant variables from the DAs of the ecological subsets and performed a composite DA at both the macro- and the meso-environmental scales. Our objective here was to derive composite models that would best distinguish reaches between the three vegetation types at both the macro- and meso-environment scales and that would also provide us with a set of predictor variables for modeling animal distributions (reported in Welsh et al. 2005). We tested the ability of our two composite models to accurately predict whether or not the data from a given reach fit a particular vegetation cover type (=classification success) using both a jackknife procedure and a resubstitution test (Anon. 1990). Cohen's kappa statistic (Titus et al. 1984) was computed for each test to indicate classification success compared with chance. For this test we adjusted the prior probabilities of group membership to equal (priors equal) because we did not know the true proportion of sites in each vegetation type in our data set prior to analysis (Anon. 1990).

Landscape-scale models for predicting stream temperature regimes

Based on the established link between vegetation patch types and differences in stream temperatures (see Results), we proposed a set of competing predictive models describing areal relationships among vegetation types (in this case forest vs grassland) and eight other catchment level variables (described above) known to be drivers of stream temperature (Poole and Berman 2001). We used all-possible-subsets regression (Anon. 1990) to test the ability of these predictor variables, and combinations thereof, to predict water temperature as represented by the August MWMT for each stream (MWMT for streams with multiple years of data were an average). We compared and selected models using Akaike's information criterion (AIC) (Burnham and Anderson 1998). We used a ten iteration cross-validation procedure that removed ten percent of the data each time, and then re-computed standard errors, to evaluate the stability of our models.

Results

Dominant vegetation assemblages (the macro-environment)

The statistical null hypothesis that the three vegetation types (mixed grassland, second-growth, and late-seral) did not vary relative to the 35 macro-environmental variables (Table 1) was rejected by our DA, supporting our research hypothesis of meaningful structural and compositional differences among these three vegetation types; informative models were derived from six of seven ecological groupings (Table 1). The best model (with the lowest Wilk's λ) for distinguishing ecological characteristics among these vegetation types was that derived from the variables describing size classes and composition of tree species, with four of six variables entered in the model (Table 1). The ground level vegetation model ranked second for best discriminating between the three vegetations (Table 1). The geographic relationships model ranked third, indicating that late-seral was generally higher in elevation than the other types, and that the second-growth sites were more often south-tending than the other types (Table 1).

The composite DA, which evaluated all 18 significant variables from each of the ecological grouping DAs (Table 1), resulted in an eight variable composite model (Fig. 3). When tested against the original site data, this composite model reclassified sites with 91.8% (resubstitution test), and a 73.5% (jackknife test) classification success (Fig. 3). Plotting actual site values for each of the two canonical variates (CV's) illustrated those variables that best distinguish each of the three vegetation types (Fig. 3). The mixed grassland sites were best differentiated from the second-growth sites by the presence of large hardwood logs in the former, and a relatively closed canopy in the latter (Fig. 3). The late-seral sites were best distinguished from the other two types by higher numbers of small hardwoods and large conifers, higher site elevations (i.e. lower, more accessible sites were harvested first), and by fewer stumps, lower percent conifer seedlings, and lower frequency of small conifers (Fig. 3). A particularly interesting result is that while our classification of the Mattole vegetation mosaic into three structurally distinct vegetation types is well supported, this analysis also demonstrates considerable overlap among these types (Fig. 3). This result, along with the similarities in species composition (especially tree species) among these plant assemblages, is evidence for a seral continuum from mixed grassland/early second-growth forest to more mature second-growth, grading into late-seral forest.

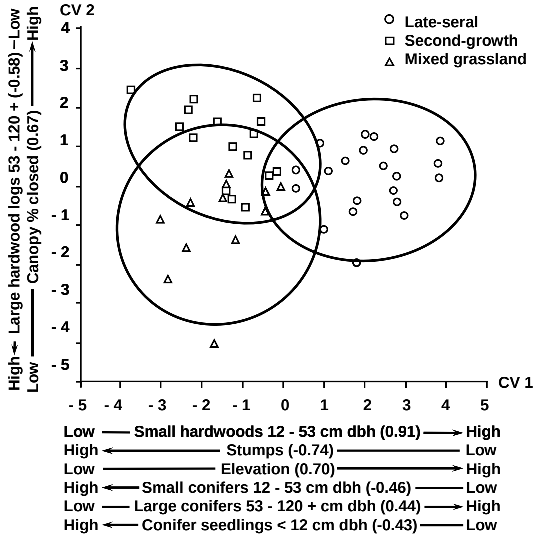

Fig. 3. Ninety-five percent confidence ellipses for sites sampled in three vegetation types of the Mattole watershed from 1994 to 1996. Canonical scores are based on a composite discriminant model derived from analysis of 35 macro-environmental variables (Table 1) measured upslope of the 49 stream reaches. The 8 variables on the two canonical axes best distinguished differences in structure and composition among the vegetation types at the macro-environmental scale. Numbers in () are standardized coefficients which indicate the relative influence of the variables on the canonical variable. Wilks' $\lambda = 0.140$; F (DF = 16, 78) = 8.156; $p = 0.0001$. Resubstitution test (% correct) = 91.84; Cohen's Kappa = 0.875; $p < 0.001$. Jackknife test (%correct) = 73.47; Cohen's Kappa = 0.593; $p < 0.001$.

The riparian/aquatic environment (the meso-environment)

Analysis of the 33 meso-environmental variables measured within the riparian reaches resulted in six of seven ecological groupings producing informative models (Table 2). The ground vegetation and ground cover models were the best at differentiating riparian environments between the three vegetation types. Percent grass and herbs were lowest within the riparian of the late-seral sites, and highest in mixed grassland sites, with values for second-growth sites intermediate (Table 2). Exposed soil was lowest in the late-seral, but nearly equally abundant in the other two types (Table 2). Stream temperatures and percent fine sediments were lowest at the late-seral sites and highest in the grassland sites, while percent large shrubs and percent boulders were highest in late-seral and lowest at either the grassland (% large shrubs) or second-growth (% boulders) sites (Table 2).

Subjecting the seven significant variables at the meso-environmental scale (Table 2) to DA resulted in a composite model of riparian conditions comprised of five variables (Fig. 4). Stream temperature and percent herb, respectively, best distinguished riparian conditions among the three vegetation types, while the variables percent exposed soil, percent boulders, and percent grassland added further discriminatory power (Fig. 4). This model had 87.5% correct resubstitution, and a 62.5% correct jackknife, success (Fig. 4).

Microclimates within dominant vegetation types

Highest mean summer air temperature (for the warmest four days in August 1997) and relative humidity values at the four late-seral riparian sites were markedly lower and higher, respectively, and more stable across all stations from streamside to 30 m perpendicular distance, showing only slight overlap at one standard error with the same measures taken at the four second-growth and four grassland riparian sites (Fig. 5a and b). These latter two sets of sites also showed markedly different mean values, but with slight overlap at one standard error for three of four stations, with the grassland sites having the highest overall air temperatures and lowest relative humidity values (Fig. 5a and b).

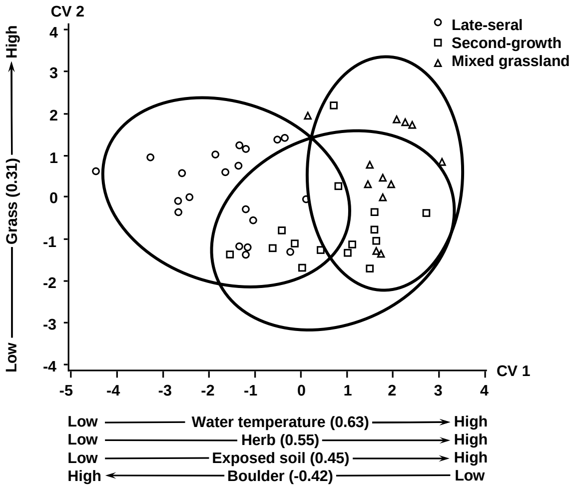

Fig. 4. Ninety-five percent confidence ellipses for riparian sites sampled in three vegetation types of the Mattole watershed from 1994 to 1996. Canonical scores are based on a composite discriminant model derived from analysis of 33 meso-environmental variables (Table 2) measured within the riparian zone of 49 stream reaches. The five variables on the two canonical axes best distinguished differences in the riparian and stream channels among the three vegetation types at the meso-environmental scale. Numbers in () are standardized coefficients which indicate the relative influence of the variables on the canonical variable. Wilks' $\lambda = 0.235$; F (DF = 10, 82) = 8.7; p = 0.001. Resubstitution test (% correct) = 87.50; Cohen's Kappa = 0.806; p = 0.001. Jackknife test (% correct) = 62.50; Cohen's Kappa = 0.410; p = 0.001.

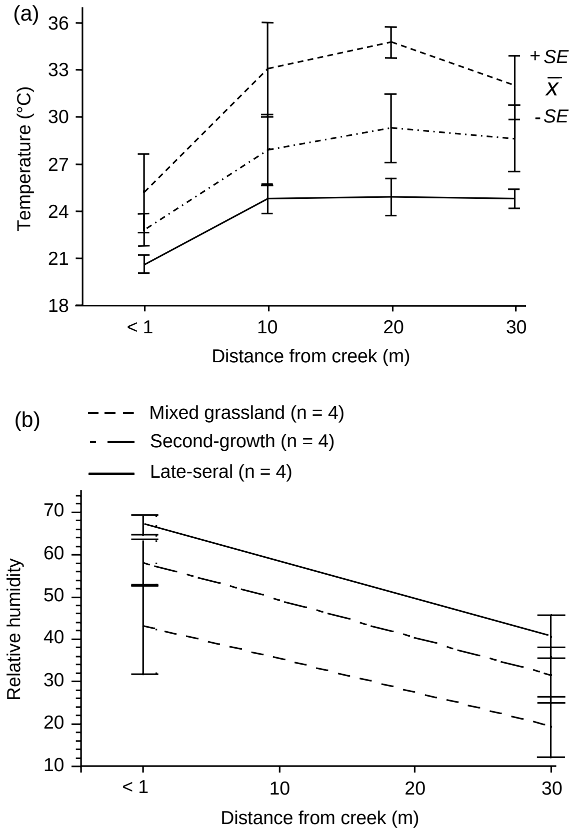

Fig. 5. a) Mean air temperatures from riparian transects of four representative stream reaches in each of the three dominant vegetation types in the Mattole watershed. Data used here were from the hottest four-day period of the summer (4–7 August) of 1997. Maximum temperatures for each of the four days were averaged for each reach, then means and standard errors were calculated within each of the vegetation types. b) Mean relative humidity (RH) from subsets of four representative stream reaches in each of the three dominant vegetation types in the Mattole watershed. Data used here were from the hottest four-day period of the summer (4–7 August) of 1997. Minimum RH's for each of the four days were averaged for each reach, then means and standard errors were calculated within each of the three vegetation type.

Landscape processes and stream temperatures

In order to examine linkages between landscape level processes and stream temperatures we tested the ability of nine landscape-scale variables, alone and in combination, to predict summer water temperature regimes (as represented by MWMT) of 40 Mattole tributaries measured over eight summers (1998–2002) using all-possible-subsets regression (Anon. 1990). The best model (lowest AICc) was: MWMT = 0.676–0.829 (aspect) + 0.060 (proportion grassland) + 1.853 (catchment area [log]) + 0.577 (August minimum air temperature) (Table 3). This model accounted for 68% of the variance (R^2 [adjusted] = 0.683) in MWMT across the 40 sample catchments over eight years (Table 3). The model was quite stable with a cross validation success of 83.6%. Eight other models had similar, though slightly higher AICc values, with mostly lower adjusted R^2 values, but all were within four AIC units of the top model (Table 3). Three of the top four models contained the variables aspect, catchment area, grass (= non-forested habitat), and August minimum air temperature (Table 3). Additional variables in subsequent models were August maximum air temperature and illumination (June) (Table 3); with this latter variable highly correlated with aspect ($r = -0.74$, $p = <0.0001$). However, the sixth ranked model (based on AICc) was the most parsimonious with only three variables; aspect, grass, and catchment area, explaining the most variation in the data with an R^2 (adjusted) of 0.69 (Table 3). We opted to include the variables from both models one and six (Table 3) in a sensitivity analysis to evaluate the relative influence of these covariates on MWMT.

To evaluate the relative influence of each of the variables in the two best models, we held the other variables in each model constant at both their minimum and maximum (e.g. aspect = either south or north; August minimum temperature = either 12.8 or 11.6°C) and re-ran the model at each extreme to determine the range of influence each non-fixed covariate had on stream temperature (MWMT) (Table 4, Fig. 6). The range of MWMT's in our dataset went from a low of

Table 3. Models for predicting water temperature (MWMT) at the sub-basin level in the Mattole Watershed. Corrected AIC (AIC_C) and adjusted R^2 are reported for competing models, and models are listed in order of smallest AIC_C. Models with vegetation covariates used the proportion of total hectares of each type in a sub-basin. The sign in parentheses indicates the relationship of that variable to water temperature (MWMT).

Model #	Model covariates	AIC_c	Akaike weights	Adj. R^2	Cross validation
1	Aspect (−) grass (+) lnarea (+) mintemp (+)	413.2	0.286	0.68	0.836
2	Aspect (−) lnarea (+) mintemp (+)	413.9	0.201	0.66	0.893
3	Aspect (−) grass (+) lnarea (+) mintemp (+) maxtemp (+)	415.1	0.110	0.68	0.851
4	Aspect (−) grass (+) illumJ (−) lnarea (+) mintemp (−)	415.5	0.090	0.68	0.859
5	Aspect (−) lnarea (+) mintemp (+) maxtemp (+)	415.6	0.086	0.65	0.925
6	Aspect (−) grass (+) lnarea (+)	416.0	0.070	0.69	0.829
7	Grass (+) lnarea (+) mintemp (−)	416.3	0.061	0.67	0.865
8	Aspect (−) grass (+) illumJ (−) lnarea (+) mintemp (−) maxtemp (+)	416.6	0.052	0.68	0.866
9	Aspect (−) lnarea (+)	417.0	0.043	0.67	0.892

11.36°C to a high of 27.93°C. Catchment area, which for the forty catchments ranged from 21.1 to 9775.1 ha, had the greatest influence on MWMT, with a change of 11.38°C across the range of catchment sizes (Table 4, Fig. 6). Proportion grass, ranging from zero to 48% across the forty catchments, was the next most influential variable, with MWMT increasing 2.86°C across its range (Table 4, Fig. 6). Aspect had the third greatest influence, with MWMT increasing 1.64°C from north to south (Table 4, Fig. 6). Minimum air temperature in August, ranging from 12.8 to 11.6°C, had the least influence, with a total change in MWMT of 0.69°C across its range (Table 4, Fig. 6).

Applying the model

Of the four variables that emerged in our best models (Table 3, Models 1 and 6), only one variable – proportion of grassland – lends itself to being manipulated by resource managers. Using stream temperature data related to coho salmon presence by sub-basin in the Mattole (Welsh et al. 2001), we compared the proportions of grassland for those catchments with and without coho detections. We found that the proportion of grassland (=unforested) habitat in catchments with coho was significantly lower than the proportion of grassland in catchments without coho ($T = 1.74$, $p = 0.049$). We applied our most parsimonious model (Table 3, Model 6) to predict what proportion of grassland at a given catchment size would maintain summer stream temperatures suitable for coho salmon. We used the threshold water temperature based on the hottest summer mean weekly average maximum temperature (MWMT) (Welsh et al. 2001) to set the upper limit of our model. Results of this analysis indicated that when non-forest or grassland exceeds 10%, south-facing catchments in the Mattole >200 ha, and north-facing catchments >400 ha, will yield stream temperatures that exceed the limits for coho salmon (Table 4, Fig. 7). The best model based on AIC_c (Table 3, Model 1) was slightly different. With aspect held due south, and

Table 4. Predictions for the best three-variable model (Table 3, Model 6) for MWMT by catchment area (ha) and proportion grassland. Bold indicates values that do not exceed the critical MWMT for coho salmon (18°C) (Welsh et al. 2001). The model is $MWMT = 6.9067 - 0.70717\ (aspect) + 0.06014\ (grass) + 1.94469\ (area[log])$.

Hectares	% Grassland						
	0	5	10	15	20	25	30
Hold ASPECT due south (0)							
25	**13.2**	**13.5**	**13.8**	**14.1**	**14.4**	**14.7**	**15.0**
50	**14.6**	**14.9**	**15.2**	**15.5**	**15.8**	**16.1**	**16.4**
100	**15.9**	**16.2**	**16.5**	**16.8**	**17.1**	**17.4**	**17.7**
200	**17.3**	**17.6**	**17.9**	18.2	18.5	18.8	19.1
400	18.6	18.9	19.2	19.5	19.8	20.1	20.4
800	20.0	20.3	20.6	20.9	21.2	21.5	21.8
1600	21.3	21.6	21.9	22.2	22.5	22.8	23.1
3200	22.7	23.0	23.3	23.6	23.9	24.2	24.5
Hold ASPECT due north (2)							
25	**11.8**	**12.1**	**12.4**	**12.7**	**13.0**	**13.3**	**13.6**
50	**13.2**	**13.5**	**13.8**	**14.1**	**14.4**	**14.7**	**15.0**
100	**14.5**	**14.8**	**15.1**	**15.4**	**15.7**	**16.0**	**16.3**
200	**15.8**	**16.2**	**16.5**	**16.8**	**17.1**	**17.4**	**17.7**
400	**17.2**	**17.5**	**17.8**	18.1	18.4	18.7	19.0
800	18.5	18.8	19.1	19.4	19.7	20.0	20.4
1600	19.9	20.2	20.5	20.8	21.1	21.4	21.7
3200	21.2	21.5	21.8	22.1	22.4	22.7	23.0

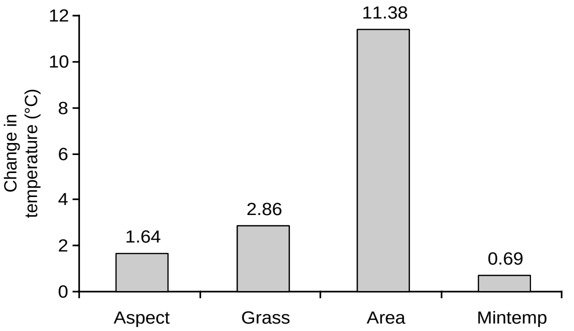

Fig. 6. Relative influence of covariates in the best models (Table 3, Models 1 and 6) for predictive water temperature (MWMT).

minimum air temperature at its highest, catchments > 200 ha with any grassland whatsoever, the model predicted that the stream temperature would exceed the threshold for coho. With aspect north and minimum air temperature at its lowest, model one predicted that catchments >400 ha with grassland >20%, the stream would exceed the thermal threshold for coho salmon. Of particular interest here for the recovery of coho salmon is the apparent upper size threshold, regardless of vegetation cover type or amount, for interior (as opposed to coastal) catchments with summer water temperatures that can support them (Table 4).

Discussion

The pattern of vegetation we found in the Mattole, when compared with the historical pattern (Fig. 2), indicated a dramatically altered watershed where the once dominant late-seral forests have been largely replaced by early succession forests and mixed grasslands. This landscape has been transformed by intensive forest harvesting, conversions of forest to agricultural lands, and a

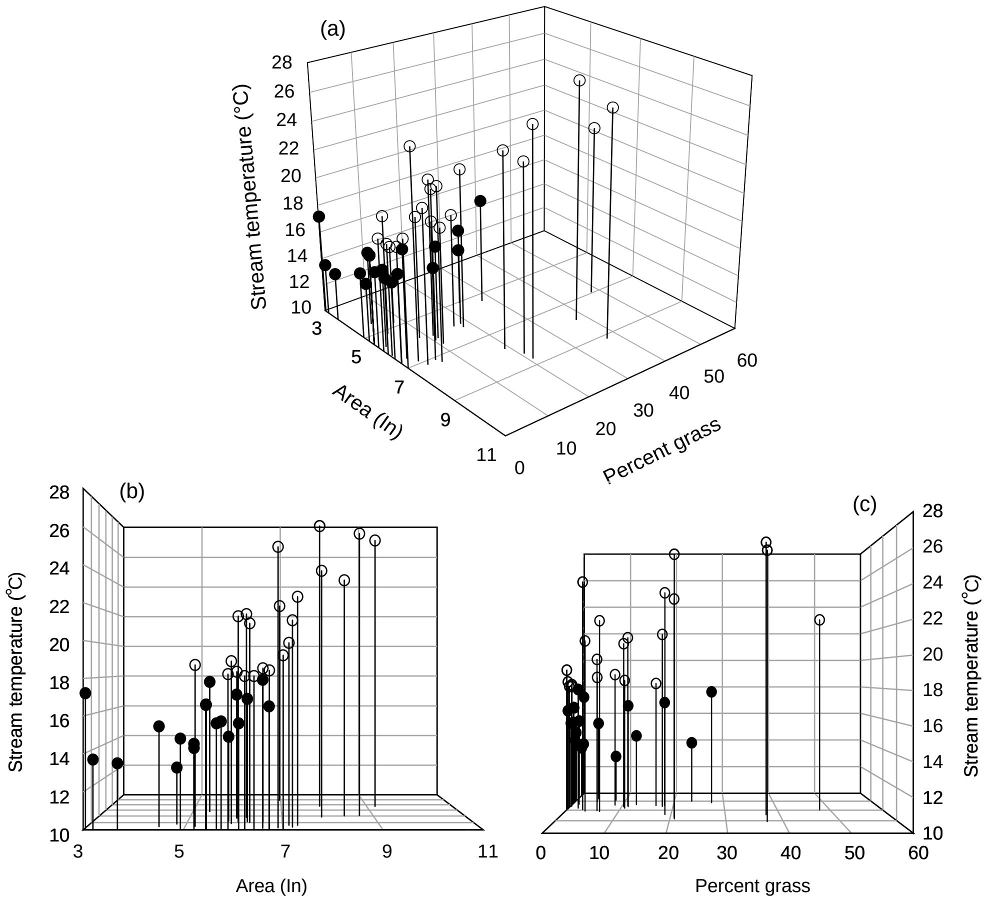

Fig. 7. Three dimensional depiction of the best landscape-scale multiple regression model for predicting stream temperature (Table 3). Area refers to sub-basin area (hectares [log-transformed]). Open circles represent those values at or above the 18°C critical thermal threshold (mean weekly average maximum temperature [MWMT]) for coho salmon in the Mattole (see Welsh et al. 2001). a) depicts the overall distribution of the data; b) depicts the data rotated to best display the effect of catchment area; c) depicts the data rotated to best display the effects of percent grassland cover.

proliferation of small homesteads with associated roads and clearings (Anon. 1989). While we cannot demonstrate a direct cause and effect relationship from these data, it would appear from the patterns that we have documented, that these landscape-level alterations have had major influences on micro-climatic conditions within riparian environments across this landscape (Fig. 5a and b). Given what we know of the historical conditions of this watershed (Fig. 2), a particularly significant effect of these changes has been a shift toward warmer water temperature regimes in many formerly cool tributaries of this watershed (see also Welsh et al. 2001). Mitchell (1999) noted that "... changes in stream temperature may affect several levels of stream organization: 1) the individual physiologically and behaviorally; 2) the population through development of the individuals' fecundity and survival; and 3) the community by favoring temperature-tolerant taxa over temperature intolerant ones, leading to shifts in community structure". He noted further "each of these levels affects the other levels (i.e. a change in community structure alters food availability to other community members, affecting individual fitness, which in turn affects the population)" (Mitchell 1999: 78).

While we found marked differences in the structure and composition of the environments within the three vegetation assemblages of the Mattole, there was also considerable overlap along this apparent seral continuum in both upland and riparian conditions (Figs. 3 and 4). We found seven of the thirteen variables that best distinguished these vegetation types from one another (Tables 1 and 2) were also good predictors of the presence of one or more of the three native herpetofaunal assemblages in the Mattole (see Table 3; Welsh et al. 2005). However, despite some overlap for several of the structural variables in these predictive models (grass appeared in nine of twelve models either positive or negative), the single best predictor of these different herpetofaunal assemblages was water temperature. Water temperature, with either a positive or negative relationship with a particular assemblage, appeared in all twelve of our models, including the best predictive model for each assemblage, and those within two AIC units of the best (Table 3; Welsh et al. 2005). Our analysis of microclimates within the three vegetation types indicated marked differences in summer air temperature, relative humidity (Fig. 5a and b) and water temperature (Fig. 3 in Welsh et al. 2005) across the three patch types. It comes as no surprise therefore that the variable that directly measured the greatest variation in this critical attribute of the microclimatic regime would be the best single predictor of the presence of particular herpetofaunal assemblages at a given location (Table 3; Welsh et al. 2005).

A complex suite of external factors ("drivers"), such as climate and landscape topography, interact with the internal structure of fluvial systems (e.g. channel, alluvial aquifer, and riparian zone) to determine how heat and water are distributed and exchanged amongst, or lost from, streams (Poole and Berman 2001). Our assessment of what drives the summer water temperature regimes in the Mattole indicates that the typical emphasis on riparian conditions alone (Mitchell 1999 and citations therein, Johnson and Jones 2000), conditions which tend only to buffer stream temperature regimes which are established by external "drivers" (Poole and Berman 2001), may be misguided and too simplistic as a single focus for the management of stream temperature regimes (see also Willson and Dorcas 2003). This may be especially true in areas of warmer climates such as California.

Contrary to the typical focus by resource managers on conditions in the riparian zone, our results indicate a strong relationship between upstream and upslope conditions of the catchment and stream temperatures. In fact, we suggest that the primary factor for determining stream temperature regime, at least for watersheds in northern California like the Mattole, with warm interior (as opposed to cooler coastal) conditions and located latitudinally in the temperate region between the warm California (a Mediterranean type climate with long hot dry summers) and the cooler Pacific Northwest climate zones, is the external driver of catchment area (Table 3, Figs. 6 and 7). Our best model consisted of four variables: aspect, catchment area, the proportion of that catchment in grassland (=non-forested) habitat, and minimum August air temperature (Table 3). Catchment area was the most influential variable in this model, with proportion grassland the second most influential variable (Figs. 6 and 7). James et al. (2003) reported both higher and less variable amounts of soil moisture in forest compared with grassland, with the net effect of vegetation on soil moisture during a drying period significantly greater in the grassland. The correlation between catchment area and the proportion grassland was low ($r = 0.46$), and a ridge regression indicated that covariance between these two variables was not an issue. However, of these four variables, only proportion grass lends itself to some management options as the others are fixed landscape parameters in any given sub-basin.

Brosofske et al. (1997) examined management effects on riparian microclimates in Washington State and reported that strong associations existed between stream temperatures and soil temperatures, even at stations well away from the stream. They concluded that microclimate changes caused by timber harvesting in the watershed, even well away from the stream, may affect the riparian microclimate and should not be ignored when developing management plans (Brosofske et al. 1997: 1197; see also Hewlett and Fortson 1982). It seems reasonable, given that summer flow derives mostly from the groundwater, where its temperature is strongly influenced by that of the bedrock and soil through which it percolates (Poole and Berman 2001), that changes in soil temperature would likely cause changes in the temperature of the groundwater emerging through that substrate, and the magnitude of the effect would be related to the soil surface (=catchment) area upstream and upslope, and less so by any travel time through the warming air subsequent to emergence. Optimum conditions for two native cold-water-adapted stream amphibians of the Mattole, the tailed frog and the southern torrent salamander (Welsh and Lind 1996, 2002), occur in ground water-charged headwater reaches where water temperatures average ca 11°C, and exhibit low (<2.0°C) daily amplitude in the summer (Welsh unpubl.). It appears to us that the recent transformation of the upland vegetation of this landscape has markedly altered both riparian microclimates and stream temperatures, and that this process has contributed to a marked decline in the native cold-water-adapted species of this watershed (see Welsh et al. 2001, 2005).

Ward (1998) and Harding et al. (1998) both documented strong relationships between landscape-scale processes, in particular past disturbance regimes, and stream and riparian biodiversity. In fact, it has become increasingly clear that past land uses have a profound and long-lasting effect on ecosystem processes (Foster et al. 2003). Chen et al. (1999), detailing the important links between coarse-scale landscape processes and available microclimates in forest ecosystems, noted the importance of a range of microclimate regimes for maintaining the species composition and ecological functions of both aquatic and terrestrial ecosystems in managed landscapes (see also Saunders et al. 1998). Understanding the effects of these coarse-scale processes on available microclimates is particularly important in order to interpret the distribution patterns of native ectothermic vertebrates (Huey and Kingsolver 1989). Our initial focus was on the question of what range of microclimates and microhabitats exist within the primary vegetation mosaic patches of the Mattole, and how might these conditions influence the distributions of the native herpetofauna. We examined the structure and internal microclimate of the primary vegetation mosaic types, and particularly the potentially species-rich riparian environments within. Our objectives were to describe the patch mosaic elements, document conditions within patch types, and then examine how these conditions might influence the distributions of native species at the watershed scale (results in Welsh et al. 2005). Here we have focused on the first two objectives, distinguishing the landscape patch mosaic elements, and describing differences in microclimates and microhabitats within each patch type. We have also discussed how differences in these conditions, manifesting at the landscape scale, can influence the distributions of the native herpetofauna. Such information can inform land managers on how better to maintain biodiversity, and in particular those sensitive species that might be most adversely impacted by alterations of the native landscape (Ward 1998, Harding et al. 1998). Furthermore, without this larger spatial scale information it is unlikely that all of the important smaller scale animal-habitat associations can be identified and maintained.

Just as medical sciences have traced causal events across several levels of organization, from gene to cell to organ to individual, ecologists strive to do the same. We have added to the understanding of factors influencing physiologically-restricted ectotherms, building on work done by others who evaluated these organisms' thermal niche and demonstrated the importance of particular riparian conditions for providing the appropriate microclimatic conditions defined by that niche, and linked the presence of those conditions to processes at the landscape scale. As such we have documented an additional and larger-scale process of the web of mutually inclusive factors influencing these species distributions and abundances. This information promotes our understanding of the interconnections across hierarchical ecological systems and thus helps us predict and detect (in the early stages) how changes at one level affect other levels, and which species are most likely to be negatively impacted by particular process disruptions or disturbance regimes (Welsh and Ollivier 1998, Welsh and Droege 2001).

Acknowledgements – We thank the many Mattole landowners who allowed us access to their lands, and Dave Fuller of the Arcata Resource Area of the Bureau of Land Management, Sanctuary Forest, Redwood Monastery, the Mattole Salmon Group, and the Mattole Restoration Council for their help and support. We thank Jay Arnold, Don Ashton, Jennifer Bamsburger, Jennifer Bloeser, Jim Dahl, Darla Elswick, Amy Lind, Luisa Molinero, Jeff Neuman, and Kary Slick for their assistance with the field work, and C. Wheeler, H. Stauffer, B. Harvey, Leslie Reid, and J. Dunk for helpful comments on earlier versions of this manuscript. Funding for this research came from the Interagency Forest Ecosystem Management and Assessment Team (FEMAT) program.

References

Anon. 1989. Elements of recovery: an inventory of upslope sources of sedimentation in the Mattole River watershed. – Report prepared by the Mattole Restoration Council for the California Dept of Fish and Game, Sacramento, CA.

Anon. 1990. SAS user's guide. – SAS Inst.

Brosofske, K. D. et al. 1997. Harvesting effects on microclimatic gradients from small streams to upland in western Washington. – Ecol. Appl. 7: 1188–1200.

Burnham, K. P. and Anderson, D. R. 1998. Model selection and inference: a practical information-theoretical approach. – Springer.

Chen, J. et al. 1999. Microclimate in forest ecosystem and landscape ecology. – BioScience 49: 288–297.

Daly, C., Neilson, R. P. and Phillips, D. L. 1994. A statistical-topographic model for mapping climatological precipitation over mountainous terrain. – J. Appl. Meteorol. 33: 140–158.

Dunham, A. E., Grant, B. W. and Overall, K. L. 1989. Interfaces between biophysical and physiological ecology and the population ecology of terrestrial vertebrate ectotherms. – Physiol. Zool. 62: 335–355.

Elliott, J. M. 1981. Some aspects of thermal stress in freshwater teleosts. – In: Pickering, A. D. (ed.), Stress and fish. Academic Press, pp. 147–170.

Foster, D. et al. 2003. The importance of land-use legacies to ecology and conservation. – Bioscience 53: 77–88.

Frank, E. C. and Lee, R. 1966. Potential solar beam irradiation on slopes: tables for 30° to 50° latitudes. – USDA Forest Service, Rocky Mountain Forest and Range Experiment Station.

Gregory, S. V. 1997. Riparian management in the 21st century. – In: Kohm, K. A. and Franklin, J. F. (eds), Creating a forestry for the 21st century. Island Press, pp. 69–85.

Harding, J. S. et al. 1998. Stream biodiversity: the ghost of land use past. – Proc. Nat. Acad. Sci. USA 95: 14843–14847.

Hewlett, J. D. and Fortson, J. C. 1982. Stream temperature under an inadequate buffer strip in the southeast Piedmont. – Water Resour. Bull. 18: 983–988.

Huey, R. B. 1982. Temperature, physiology, and ecology of reptiles. – In: Gans, C. and Pough, H. (eds), Biology of the Reptilia Vol. 12 Physiology C. Academic Press, pp. 25–91.

Huey, R. B. 1991. Physiological consequences of habitat selection. – Am. Nat. 137 (suppl.): 90–115.

Huey, R. B. and Kingsolver, J. G. 1989. Evolution of thermal sensitivity of ectotherm performance. – Trends Ecol. Evol. 4: 131–135.

Hutchison, V. H. and Dupre, R. K. 1992. Thermoregulation. – In: Feder, M. and Burggren, W. H. (eds), Environmental physiology of the amphibians. Univ. of Chicago Press, pp. 206–249.

James, S. E. et al. 2003. Temporal heterogeneity of soil moisture in grassland and forest. – J. Ecol. 91: 234–239.

Johnson, S. L. and Jones, J. A. 2000. Stream temperature responses to forest harvest and debris flows in western Cascades, Oregon. – Can. J. Fish. Aquat. Sci. 57 (suppl. 2): 30–39.

Magnuson, J. J., Crowder, L. B. and Medvick, P. A. 1979. Temperature as an ecological resource. – Am. Zool. 19: 331–343.

Mitchell, S. 1999. A simple model for estimating mean monthly stream temperatures after riparian canopy removal. – Environ. Manage. 24: 77–83.

Moyle, P. B. and Yoshiyama, R. M. 1994. Protection of biodiversity in California: a five-tiered approach. – Fisheries 19: 6–118.

Naiman, R. J., Decamps, H. and Pollack, M. 1993. The role of riparian corridors in maintaining regional biodiversity. – Ecol. Appl. 3: 209–212.

Naiman, R. J. et al. 1998. Riparian forests. – In: Naiman, R. J. and Bilby, R. E. (eds), River ecology and management: lessons from the Pacific coastal ecoregion. Springer, pp. 289–323.

Perry, D. A. and Amaranthus, M. P. 1997. Disturbance, recovery, and stability. – In: Kohm, K. A. and Franklin, J. F. (eds), Creating a forestry for the 21st century. Island Press, pp. 31–56.

Poole, G. C. and 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.

Saunders, S. C. et al. 1998. Hierarchical relationships between landscape structure and temperature in a managed forest landscape. – Landscape Ecol. 13: 381–395.

Schrader-Frechette, K. S. and McCoy, E. C. 1993. Method in ecology: strategies for conservation. – Cambridge Univ. Press.

Sokal, R. R. and Rohlf, F. J. 1981. Biometry. – W. H. Freeman.

Stouder, D. J., Bisson, P. A. and Naimen, R. J. (eds) 1997. Pacific salmon and their ecosystems. – Chapman and Hall.

Titus, K., Mosher, J. A. and Williams, B. K. 1984. Chance-corrected classification for use in discriminant analysis: ecological applications. – Am. Midl. Nat. 111: 1–7.

Toft, C. A. 1991. Reply to Seaman and Jaeger: an appeal to common sense. Points of view: a controversy in statistical ecology. – Herpetologica 46: 357–361.

Ward, J. V. 1998. Riverine landscapes: biodiversity patterns, disturbance regimes, and aquatic conservation. – Biol. Conserv. 83: 269–278.

Welsh, H. H. Jr 1994. Bioregions: an ecological and evolutionary perspective and a proposal for California. – California Fish and Game 80: 97–124.

Welsh, H. H. Jr and Lind, A. J. 1995. Habitat correlates of the Del Norte salamander, *Plethodon elongatus* (Caudata: Plethodontide), in northwestern California. – J. Herpetol. 29: 198–210.

Welsh, H. H. Jr and Lind, A. J. 1996. Habitat correlates of the southern torrent salamander, *Rhyacotriton variegatus* (Caudata: Rhyacotritonidae), in northwestern California. – J. Herpetol. 30: 385–398.

Welsh, H. H. Jr and Ollivier, L. M. 1998. Stream amphibians as indicators of ecosystem stress: a case study from California's redwoods. – Ecol. Appl. 8: 1118–1132.

Welsh, H. H. Jr and Droege, S. 2001. A case for using Plethodontid salamanders for monitoring biodiversity and ecosystem integrity of North American forests. – Conserv. Biol. 15: 558–569.

Welsh, H. H. Jr and Lind, A. J. 2002. Multiscale habitat relationships of stream amphibians in the Klamath-Siskiyou Region of California and Oregon. – J. Wildl. Manage. 66: 581–602.

Welsh, H. H. Jr, Roelofs, T. D. and Frissell, C. A. 2000. Aquatic ecosystems of the redwood region. – In: Noss, R. F. (ed.), The redwood forest: history, ecology, and conservation of the coast redwoods. Island Press, pp. 165–199.

Welsh, H. H. Jr et al. 2001. Distribution of juvenile coho salmon (*Oncorhynchus kisutch*) in relation to water temperatures in tributaries of the Mattole River, California. – N. Am. J. Fish. Manage. 21: 464–470.

Welsh, H. H. Jr, Hodgson, G. R. and Lind, A. J. 2005. Ecogeography of the herpetofauna of a northern California watershed: linking species patterns to landscape processes. – Ecography 28: 521–536.

Wiens, J. A. 1996. Wildlife in patchy environments: metapopulations, mosaics, and managements. – In: McCullough, D. R. (ed.), Metapopulations and wildlife conservation. Island Press, pp. 53–84.

Willson, J. D. and Dorcas, M. E. 2003. Effects of habitat disturbance on stream salamanders: implications for buffer zones and watershed management. – Conserv. Biol. 17: 763–771.