

Distribution of Juvenile Coho Salmon in Relation to Water Temperatures in Tributaries of the Mattole River, California

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Abstract.—In an attempt to define the upper thermal tolerance of coho salmon *Oncorhynchus kisutch*, we examined the relationship between the presence of this species and the summer temperature regime in 21 tributaries of the Mattole River of northwestern California. We characterized the temperature regime of each tributary by determining the highest average of maximum daily temperatures over any 7-d period (maximum weekly maximum temperature, MWMT) and the highest average of mean daily temperatures over any 7-d period (maximum weekly average temperature MWAT), by the use of hourly measurements throughout the summer. Coho salmon presence was determined by divers in late summer. Both variables that were used to describe the temperature regime provided good-fitting models of the presence or absence of coho salmon in separate logistic regressions, and both correctly determined the presence or absence in 18 of 21 streams, given the previous probability of a 50% likelihood of coho salmon presence. Temperature regimes in the warmest tributaries containing juvenile coho salmon had MWMT of 18.0°C or less or MWAT of 16.7°C or less; conversely, all of the streams where MWMT was less than 16.3°C or MWAT was less than 14.5°C contained juvenile coho salmon. These results, combined with historical and current watershed conditions that affect stream temperatures, suggest that management strategies to restore and conserve coho salmon in the Mattole River drainage should focus on the water temperature regime. Such a focus is also likely to benefit other declining species requiring cold water, including the tailed frog *Ascaphus truei* and southern torrent salamander *Rhyacotriton variegatus*.

The physical environment is the basic template for all life processes where organisms evolve and persist (or not) through time (Southwood 1977, 1988). Consequently, maintaining the physical environment within the range of conditions conducive to the persistence of the native biota is a logical basis for managing ecosystem integrity (Swanson et al. 1997). Ectothermic organisms, because they have limited physiological means to control and regulate body temperatures, are particularly dependent on the thermal environments in which they have evolved to persist (e.g., Dunham et al. 1989; Hutchison and Dupre 1992; Rome et al. 1992). The thermal niche as an ecological resource (as in Magnuson et al. 1979; see also Huey 1991) is that range of temperatures within which an organism is able to persist.

Forest- and stream-dwelling organisms in the Pacific Northwest have evolved in landscapes that have in recent geologic time been dominated by

coniferous forests (Axelrod 1976; Daubenmire 1978). Climatic regimes in the riparian and aquatic environments within these forests, in the absence of major natural or anthropogenic disturbances, are typically cool and humid (Chen et al. 1999). Stream-dwelling organisms, such as the fishes and stream amphibians of the Pacific Northwest, have evolved and adapted to thermal niches providing relatively stable, cold water temperatures (e.g., Elliott 1981; Welsh 1990; Welsh and Lind 1996). However, changes in forest seral stage or canopy structure can have profound effects on riparian and stream microclimatic regimes (Beschta et al. 1987). For example, logging can alter stream environments and associated microclimates such that they no longer support native species (Brown and Krygier 1970; Brosofske et al. 1997; Mitchell 1999).

Managing landscapes of the Pacific Northwest to maintain fish and amphibians requires understanding the physiological tolerances of these species and any critical temperature-dependent ecological interactions (e.g., Crowder and Magnuson 1983). This information must then be integrated

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Received January 14, 2000; accepted October 30, 2000

with knowledge of the range of effects that land management may have on stream temperatures. Unfortunately, many fish and amphibians in the Pacific Northwest are already threatened by habitat alterations over much of their ranges (e.g., Welsh 1990; Nehlsen et al. 1991; Frissell 1993; Frissell et al. 1997; Welsh et al. 2000). Consequently, we need to rapidly acquire information on the thermal tolerances of these species to inform managers for decision making.

A logical approach to this need is to measure environmental temperatures wherever extant populations are found to define a field-based thermal niche. In this paper we describe the use of this approach to determine the upper thermal tolerance of juvenile coho salmon *Oncorhynchus kisutch* in the Mattole River watershed of northwestern California. We believe this approach can also provide upper thresholds of tributary temperatures useful for the restoration of other declining members of the native biota of the Mattole River watershed. Because of their physiological limits, sensitivity to habitat perturbations, and the time required to reach smolt size, juvenile coho salmon may be acceptable surrogates (Caro and O'Doherty 1999) for other coldwater-adapted biota in northwestern California. Juvenile fish are particularly sensitive to extreme temperatures (Huey 1991). Consequently, designing a watershed restoration strategy based on the thermal requirements of juvenile coho salmon could provide a logical basis for establishing maximum thresholds of stream temperatures in suitable tributaries and thereby assure suitable thermal regimes for other members of the stream community that have also evolved in a coldwater regime. The establishment and use of locally determined thresholds as performance criteria in the monitoring and adaptive management of ecosystems are critical to restoring healthy systems (Mulder et al. 1999).

Study Area

The Mattole River watershed of northwestern California (hereafter the Mattole) lies in the North Coast Bioregion of California (Welsh 1994) in Humboldt and Mendocino counties, between 39°57' and 40°25' north latitude and 123°52' and 124°21' west longitude. The Mattole covers 787 km² and ranges in elevation from its estuary to 1,245 m. The common plant associations within the Mattole include the following: (1) redwood forest *Sequoia sempervirens* (in the headwaters), (2) mixed Douglas fir *Pseudotsuga menziesii* and hardwood (primarily tan oak *Lithocarpus densiflo-*

rus and madrone *Arbutus menziesii*) forest, (3) mixed chaparral (primarily manzanita *Arctostaphylos* spp., mountain whitethorn *Ceanothus cordulatus*, scrub oak *Quercus berberidifolia*, and coyote brush *Baccharis pilularis*), and (4) grasslands. Riparian zones of the Mattole, in addition to the above, also contain big leaf maple *Acer macrophyllum*, red alder *Alnus rubra*, cottonwood *Populus fremontii*, Oregon ash *Fraxinus latifolia*, and willow *Salix* spp.

The Mattole is a particularly suitable location to examine the link between thermal regime and coho salmon presence because it is near the Southern limit for this species, an area where the potential for thermal stress is likely to be the greatest. The Mattole also presents a wide range of thermal environments from cool, shaded, headwater streams to major tributaries traversing predominantly open grasslands. In addition, the Mattole has a long history of natural resource extraction from tan oak and redwood logging industries in the early 1900s to extensive harvesting of Douglas fir forests from post-World War II until the present. Since the 1800s, it also has supported sheep and cattle grazing, orchard planting, and farming. Late-seral forests, which once dominated the Mattole, have been reduced by 94% (Mattole Restoration Council 1995).

Methods

We monitored summer stream temperatures in 21 first- to fourth-order tributaries of the Mattole (Figure 1) for 1-5 years starting in 1994. These tributaries drained an average of 1,457 ha (range, 24-5,981 ha). Although we were able to investigate streams throughout the drainage that traversed all vegetation types, limited access prevented random selection of study sites. To more efficiently gather information relevant to the presence or absence of coho salmon, we undersampled extremely warm tributaries relative to their abundance. However, one of us (M.R.R.) has censused coho salmon in 60 of the 73 Mattole River tributaries and knows of no accessible tributaries containing coho salmon that are not in this data set. Stream temperatures were collected hourly for each stream over the entire summer (June-September), which we assumed would capture the highest annual values. We placed temperature loggers at depths of 30-50 cm in shaded, well-mixed areas near tributary mouths.

We conducted fish sampling during late summer, after peak water temperatures in August. We assumed that the presence of coho salmon at this

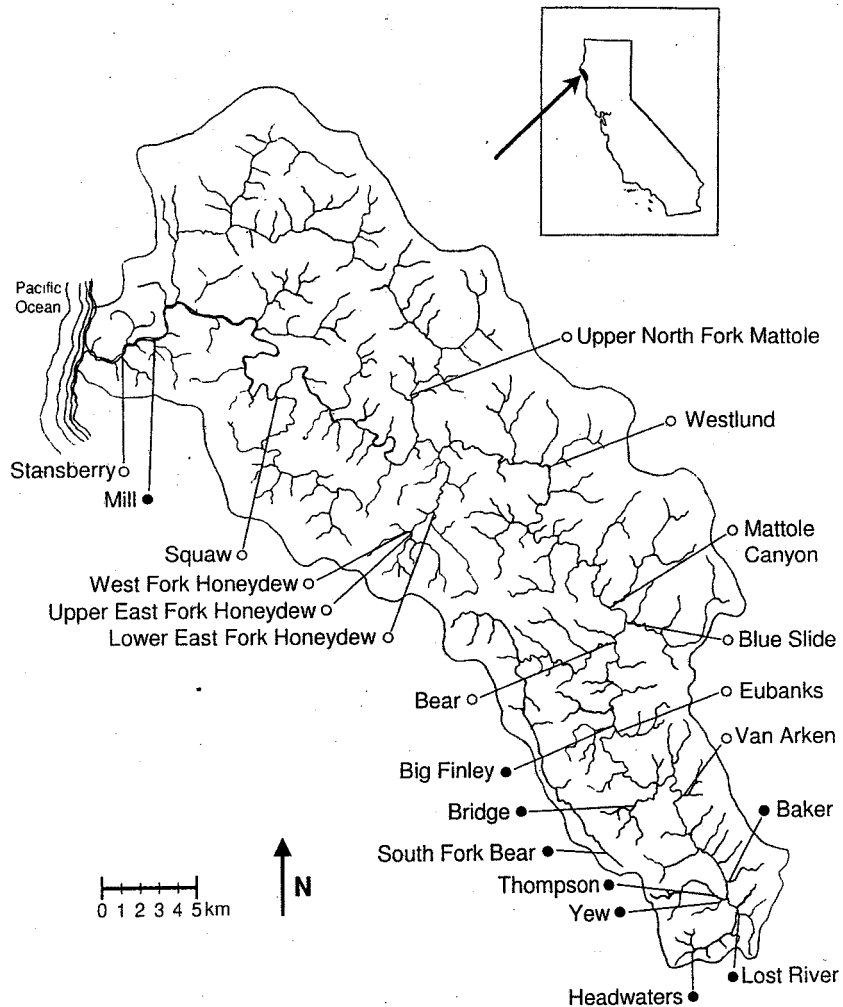


FIGURE 1.--Location of the Mattole River watershed in northwestern California (see inset) and the distribution of the 21 tributaries included in this study. Filled circles indicate the presence of coho salmon; open circles indicate no detections.

time indicated that a tributary provided year-round rearing habitat. Teams of two to three divers determined the presence of coho salmon. Coho salmon were assumed to be absent in a tributary if they were not observed after sampling in at least the first 10 pools judged to provide appropriate habitat; a single detection constituted presence. In the steep topography of the Mattole, the lower tributary reaches containing the first 10 pools usually represented the best, most-accessible habitat for fish, so we assumed that the absence of coho salmon there was a good indication of their absence farther upstream. We used data gathered in 1997-1999, when temperature data and fish observations from the same year were available for at least one year in all 21 tributaries.

We used two different variables to summarize the water temperature regime in the streams because both are currently used in the literature, and it is useful and informative to compare them in a management context. First, we averaged daily maximum temperatures for each 7-d period and then selected the highest average for the entire summer (maximum weekly maximum temperature, MWMT). Second, we averaged daily mean temperatures for each 7-d period and selected the highest average for the summer (maximum weekly average temperature, MWAT). Comparing streams with multiple years of data indicated little annual variation in MWMT, MWAT, or the presence or absence of coho salmon (for 15 streams with both 1998 and 1999 data, the correlation between years

TABLE 1.-Classification results for logistic regression models predicting coho salmon presence or absence on the basis of the maximum weekly maximum temperature (MWMT) and the maximum weekly average temperature (MWAT) and assuming a 50% probability of detecting coho salmon in a given stream. Separate analyses of MWMT and MWAT produced the same classification results.

Observed	Classified		Total
	Coho salmon present	Coho salmon absent	
Coho salmon present	8	1	9
Coho salmon absent	2	10	12
Total	10	11	21

was $r = 0.97$ and the mean difference equaled 0 for MWMT, and r equaled 0.99 and the mean difference equaled 0.8°C for MWAT). Therefore we averaged MWAT and MWMT values for our analyses when multiple years of temperature and fish data were available. We then analyzed the presence

or absence of coho salmon in separate logistic regressions by the use of MWMT and MWAT (SAS 1988).

Results

We found coho salmon in 9 of the 21 streams sampled (Figure 1), and both independent variables (MWMT and MWAT) provided good-fitting logistic models for the presence or absence of coho salmon (MWMT model: intercept = 20.77, coefficient = -1.19, $r^2 = 0.70$, and $P = 0.049$; MWAT model: intercept = 20.86, coefficient = -1.29, $r^2 = 0.65$, and $P = 0.046$). Assuming a 50% probability of finding coho salmon in a given tributary, both logistic models correctly classified 18 out of 21 streams (Table 1). Two of the three streams misclassified by the logistic regressions lacked coho salmon (Figure 2). None of the 10 streams sampled that had MWMT greater than 18.0°C contained coho salmon (Figure 2a). Similarly, they were absent from all 9 streams sampled that had MWAT greater than 16.7°C (Figure 2b). The four

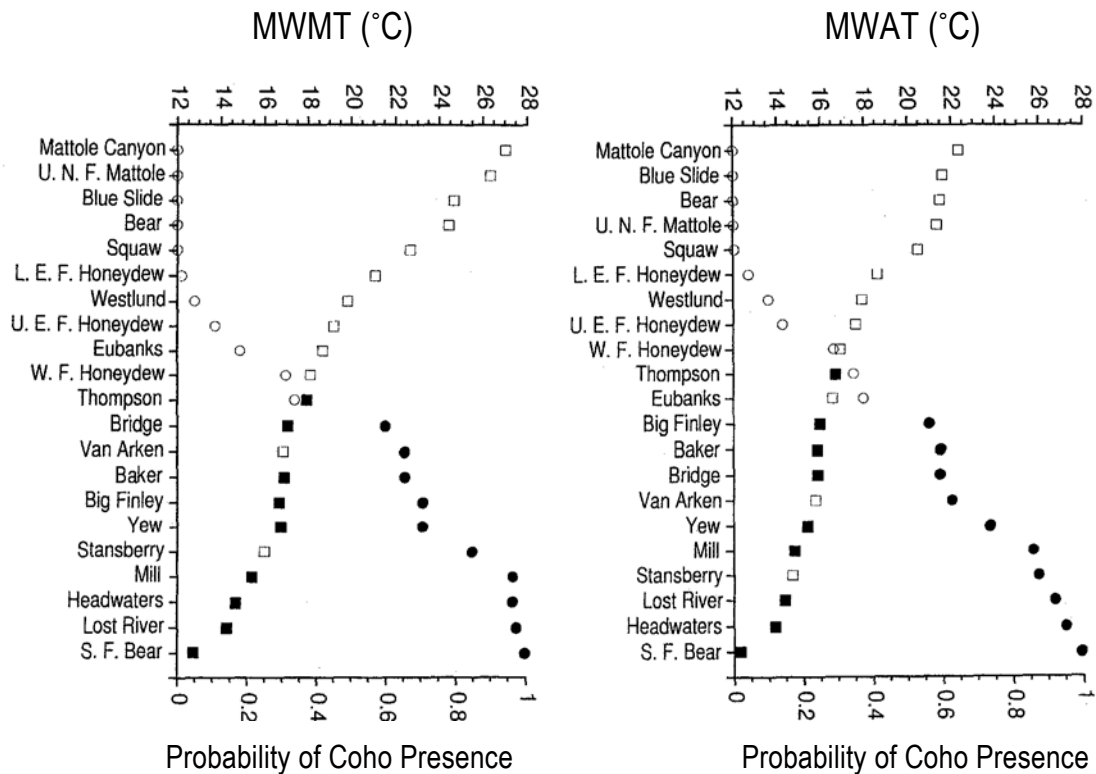


FIGURE 2.-Logistic regression of coho salmon presence or absence in 21 tributaries of the Mattole as predicted by (a) the maximum weekly maximum temperature (MWMT) and (b) the maximum weekly average temperature (MWAT). Data points for the independent variable (MWMT or MWAT) indicate the actual presence (filled squares) or absence (open squares) of coho salmon. Data points representing the probability of coho salmon presence indicate the predicted presence (filled circles) or absence (open circles). Abbreviations are as follows: L. E. F. = Lower East Fork, S. F. = South Fork, U. E. F. = Upper East Fork, U. N. F. = Upper North Fork, and W. F. = West Fork.

coldest streams on the basis of MWMT ($<16^{\circ}\text{C}$) and the three coldest streams on the basis of MWAT ($<14.5^{\circ}\text{C}$) all contained coho salmon.

Discussion

The thermal regimes of Mattole River tributaries supporting coho salmon appear to conflict with published information on the thermal tolerances of this species. For example, by the use of a database with observations from throughout the United States, Eaton et al. (1995) estimated that the maximum temperature tolerance for coho salmon is 23.4°C , which is 95% of MWAT values for locations where coho salmon were found. However, the records in the database used by Eaton et al. (1995) apparently consisted primarily of observations from larger streams and rivers. The presence of coho salmon in larger streams may reflect the ability of smolts and adults to use such streams as migration corridors rather than the ability of younger fish to use them as nursery areas. Bisson et al. (1988) observed high rates of production of coho salmon that were stocked in Washington streams that exceeded 24.5°C for more than 100 h and reached 29.5°C . These observations may be explained by extremely high productivity in those streams combined with relatively low abundances of other fishes. In most streams that naturally contain coho salmon, lower macroinvertebrate production would reduce the ability of coho salmon to maintain the high metabolic rates dictated by such high temperatures. Also, near the southern extent of their range (including all tributaries they occupy in the Mattole), coho salmon commonly co-occur with relatively abundant steelhead *O. mykiss*. Harvey and Nakamoto (1996) observed a negative relationship between the growth rate of age-0 coho salmon and the density of steelhead in two California streams similar to many of the tributaries of the Mattole River. Temperature-dependent competition between these two species may limit the thermal tolerance of coho salmon in natural streams. Finally, thermal regimes in streams supporting coho salmon in the Mattole do not approach the critical thermal maxima for this species determined by short-term laboratory and field tests (e.g., Konecki et al. 1995), which have exceeded 29°C . Clearly, long-term survival and growth under natural conditions where food may be limiting and competitors are present may be possible only in a narrower range of temperatures than can be tolerated under artificial conditions for brief periods.

Both variables used to summarize upper thermal

limits provided good-fitting models of coho salmon presence or absence. All of the streams we sampled where MWMT was less than 16.3°C or MWAT was less than 14.5°C contained coho salmon. Slightly higher values are likely to be suitable for coho salmon because of the species' consistent presence in several Mattole streams with MWATs in this range. The absence of coho salmon in tributaries with temperatures in this range is probably unrelated to temperature. For example, the absence of coho salmon in Stansberry Creek (MWAT = 14.7°C) during this study may be explained by the inaccessibility of the creek to fish at some flows. Van Arken Creek (MWAT = 15.8°C) lacked not only coho salmon but any aquatic vertebrates. The Van Arken Creek watershed is owned by a timber company and may be affected by herbicide treatments.

This study also suggests that MWMT greater than 18.1°C or MWAT greater than 16.8°C may preclude the presence of coho salmon in the Mattole. It seems very unlikely that streams with temperatures above these thresholds could provide appreciable rearing habitat for coho salmon in the absence of extremely high food availability, which might mitigate elevated metabolic rates of fish in these streams (Bisson et al. 1988). Bioenergetic benefits of water temperatures among the coldest measured in this study have been observed in other species of *Oncorhynchus*, particularly in situations in which fish do not achieve maximum food consumption (Brett et al. 1969; Railsback and Rose 1999).

Although these temperatures imply an upper limit for coho salmon in the Mattole, they cannot serve as goals or targets for particular streams without consideration of historical thermal regimes in those streams in the absence of management activities. For example, in the Mattole, natural spatio-temporal variation in watershed processes and vegetation probably yielded many streams too warm for coho salmon. However, in watersheds where human activities have clearly altered the thermal regime to the detriment of coldwater-adapted species such as coho salmon, our models could provide guidelines for thermal regimes to achieve via restoration efforts such as riparian tree planting. Our results also could provide the basis for protection of existing riparian vegetation that influences water temperature in streams with coho salmon or in streams where an analysis of previous conditions suggests that appropriate thermal regimes for coho salmon once existed.

Upstream reaches of six of the tributaries of the Mattole containing coho salmon also support the few

remaining populations of two coldwater-adapted stream amphibians in the Mattole, the tailed frog *Ascaphus truei* and the southern torrent salamander *Rhyacotriton variegatus* (H. H. Welsh and G. A. Hodgson, unpublished data), both species of special concern in California (Jennings and Hayes 1994). The presence of these amphibians in streams with juvenile coho salmon supports the idea that the latter are a possible surrogate species (Landres et al. 1988; Simberloff 1998; Caro and O'Doherty 1999) for other members of the coldwater-adapted biota of the Mattole. However, these amphibians may require cooler thermal regimes than coho salmon and commonly occupy smaller channels and springs in cooler upstream habitats inaccessible to fish (Welsh et al. 2000). In the four Mattole reaches containing tailed frogs, MWMT averaged 14.6°C, and MWAT averaged 13.8°C. In the two reaches containing southern torrent salamanders, MWMT averaged 14.5°C, and MWAT averaged 13.8°C. Summer stream temperature data from across the southern range of both amphibian species indicated that the maximum temperature at which they occurred was 15°C (Welsh and Lind 1996; H. H. Welsh and A. J. Lind, unpublished data). Recognizing the common pattern of decreasing water temperatures as one approaches headwater sources, we believe the relationship of coho salmon presence or absence and water temperature observed in this study might guide conservation and restoration activities in the Mattole to the benefit of other species adapted to cooler thermal regimes.

Acknowledgments

We thank the Arcata District of the U.S. Department of the Interior, the Bureau of Land Management, and particularly Dave Fuller for his support of this project. The help, encouragement, and support of the Mattole Salmon Group were also vital to this research. We also thank the Sanctuary Forest, the Mattole Restoration Council, and the many Mattole landowners who granted us access to their property and otherwise facilitated this project.

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