Stream Temperature and Aquatic Habitat: Fisheries and Forestry Interactions

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ABSTRACT   The temperature of water entering a forest stream system typically resembles that of the watershed's subsoil environment. As this water continues to flow down the stream system, seasonal and diurnal water temperatures are strongly influenced by solar radiation. Pronounced differences in stream temperature patterns are evident for streams draining watersheds throughout the Pacific Northwest. Seasonal and diurnal patterns of stream temperature influence a wide range of responses by instream biota. Furthermore, logging activities can initiate pronounced temperature changes by the removal of forest vegetation along channels. Buffer strips of forest vegetation are an effective means of minimizing stream temperature impacts associated with logging. Although direct mortality of fish is probably not a major concern throughout the Pacific Northwest when stream temperatures are altered by management activities, temperature changes can influence rates of egg development, rearing success, species competition, and other factors.

The temperature of water in forest streams is an important factor regulating aquatic life. But until the 1960s, the impact of harvesting on the temperature of forest streams was seldom considered or reported in the literature. Whereas fisheries studies focused on the toxicological effects of high temperature in the laboratory, most watershed studies were concerned with changes in runoff and sediment.

The situation changed dramatically in the early 1960s, especially in the Pacific Northwest. Scientists observed changes in the migration of anadromous fish in the Columbia River because of increases in temperature below dams and the outfall of the Hanford thermonuclear reactor. Conversely, the beneficial impact of dams in reducing water temperature became an issue on the Rogue River in Oregon. Research on the energy balance of large rivers began to provide information about how their temperature was affected by the macro- and microclimatic factors, storage and release from reservoirs, and localized heat inputs.

The Alsea Watershed Study in western Oregon, which began in 1958, was the first detailed study of effects of timber harvesting on the temperature of small, forest streams. Temperature changes were

monitored before and after harvesting, and research on energy balance components provided a basis for understanding why temperature changes occurred. In the late 1960s, high postlogging stream temperatures were a central issue in a harvesting-fisheries controversy over the North Umpqua River in Oregon. This controversy, along with others, was part of a developing environmental awareness and involvement by the public, administrators, and legislators. These concerns also led to major changes in national policy for the USDI Bureau of Land Management and USDA Forest Service and were instrumental in the development of forest practices acts, on a state-by-state basis, for the Pacific Northwest in the early 1970s. These forest practices acts identify management activities intended to prevent significant temperature changes in fish-bearing streams.

The objectives of this paper are to characterize stream temperature regimes in forested ecosystems, to indicate the underlying physical mechanisms of temperature change resulting from the removal of forest canopies over streams, and to identify the various processes by which temperature changes following logging can affect aquatic communities and the production of fish.

STREAM TEMPERATURES AND FORESTED ECOSYSTEMS

The temperature of moisture arriving at a channel is dependent on many factors. In high mountain catchments of the Pacific Northwest, much of the annual precipitation occurs as snowfall, which accumulates on a watershed until sufficient energy is available for snowmelt. Most snowmelt typically occurs during the spring months. However, at lower elevations snowfall accumulations may be relatively transient, and rapid snowmelt can occur during rain-on-snow events. Typically, meltwater (at $0^{\circ}C$) and rainfall (at $\geq 0^{\circ}C$) infiltrate forest soils and then move laterally through relatively porous soils and subsoils toward topographic depressions and stream channels. The pathways by which subsurface flow reaches a channel are highly variable, but when such water eventually enters a defined channel and becomes streamflow, its temperature generally reflects that of the watershed's subsoil environment.

As water flows downstream, its temperature will continue to change as a result of several factors that make up the heat balance of water. The net rate of gain or loss by a stream as it moves through a forest is the algebraic sum of net radiation, evaporation, convection, conduction, and advection (Brown 1983). Net radiation is generally dominated by the amount of direct-beam solar radiation that reaches a stream's surface. Heat gain or loss from evaporation and convection depends on the vapor pressure and temperature gradients, respectively, between the water surface and the air immediately above the surface. Wind speed at the air-water interface is also an important controlling variable. Conduction of heat between the water in the stream and the streambed depends on the type of material that makes up the bed. Bedrock channels are more efficient than gravel-bed channels at conducting heat. Advection is the result of heat exchange as tributaries or groundwater of different temperature mixes with the main streamflow, and can either increase or decrease stream temperature.

Channel characteristics and morphology also influence the amount of heat gain or loss of a stream. The surface area over which energy transfers take place is important: wide streams receive more energy than narrow ones. Discharge is another significant variable: for the same surface area and energy input, the temperature change expected of a high-discharge stream will be less than that of a low-discharge stream. In other words, for a given rate of net input, the change in temperature of a stream is directly proportional to surface area and inversely proportional to discharge.

How do these factors combine to produce temperature patterns for coastal streams in the Pacific Northwest? In winter, solar radiation levels at the stream surface are typically low, regardless of canopy cover. This is the result of a combination of factors affecting the availability of direct-beam solar radiation: short days, low sun angles (this maximizes reflection at the water surface and the shading effects of streamside vegetation and topography), and cloudy weather. During the summer months, when solar radiation levels are greatly increased (higher sun angles, longer days, and clear skies) and stream discharge is low, shading effects of the forest canopy become significant. The seasonal progression of potential direct solar radiation (for clear weather conditions) is shown in Figure 1. Although some losses occur as solar energy is routed through the atmosphere, much of the incoming solar radiation is intercepted by the canopy of streamside vegetation. Net radiation underneath a continuous canopy may be only 15% or less than that of an unshaded stream (Brown 1983) during daytime conditions. Throughout the year, evaoporative and convective transfers of energy are typically low for forested streams, because vapor pressure and temperature gradients close to the water surface are small and wind speeds are usually low. Likewise, conductive heat transfers are usually insignificant (Brown 1969). Because water has a relatively high specific heat, seasonal and daily temperature changes of forested streams are relatively small and gradual.

Seasonal temperature patterns for three small forested streams in the Pacific Northwest are shown in Figure 2. As expected, the watersheds show maximum temperatures occurring in summer and minimums in winter. However, the exact timing and magnitude of seasonal extremes vary. Porcupine Creek, the farthest north of the three, has the greatest range in monthly stream temperatures (nearly 13°C). The timing of summer maximum temperature for these streams follows, by one to two months, the timing of maximum solar radiation (Figure 1). An exception to the cyclical pattern of seasonal temperatures, shown in Figure 2, occurs in streams fed by large springs or groundwater sources. These systems often display a nearly uniform temperature year round, being cooler than other streams in summer and warmer in winter (Minkley 1963).

Characterizing the extent of natural or climatic variability in stream temperatures is an important preliminary step in attempting to document the effects that temperature changes related to logging may have on aquatic communities. If, after logging, stream temperatures lie within the bounds of natural variability, then any effects related to temperature change might be difficult to detect. Furthermore, even if
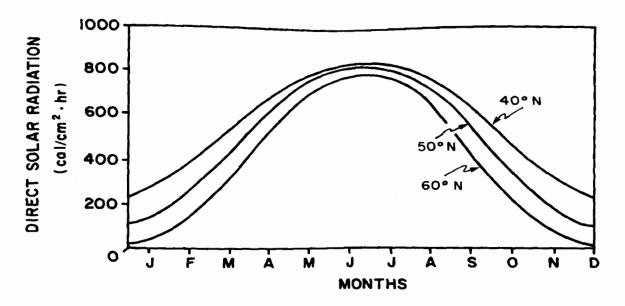
Figure 1.   Seasonal pattern of potential direct-beam solar radiation at a stream surface during clear weather (assumed atmospheric transmission coefficient = 0.9) for selected latitudes (Buffo et al. 1972).
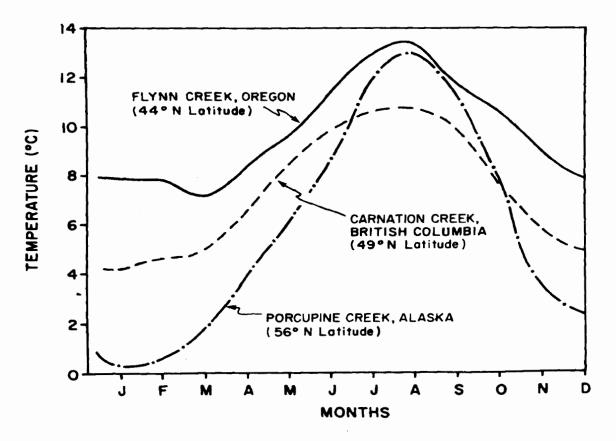

Figure 2.   Seasonal temperature patterns for three coastal streams in the Pacific Northwest.

measurable, such effects might be relatively unimportant if they would be expected to result from climatic variability anyway.

The variation in monthly temperature between years can be as much as 4°C during the winter months (December-March) for Porcupine Creek in southeastern Alaska, but year-to-year variations in monthly temperature are generally less than 2°C for other times of the year (Koski 1984). Monthly temperature fluctuations between years generally remain lower than 2°C, regardless of season, at Flynn Creek in the Oregon Coast Range.

Superimposed on the seasonal progression of stream temperatures is a diurnal pattern. Generally, changes in water temperature over the course of a day tend to be greatest during summer, in part because of the relatively low volumes of water flowing in streams at that time of year. Peak daily temperatures are usually achieved during the late afternoon, and minimums just before dawn. Even in midsummer, when large diurnal changes in direct solar radiation occur above the forest canopy, the shading effects of the forest vegetation greatly moderate and reduce the energy exchanges at the stream surface. For example, diurnal temperature variations near the mouth of Carnation Creek (Vancouver Island, British Columbia) average approximately 1.3°C for the months of June, July, and August; maximum diurnal variations for these same months are less than 2.4°C (Holtby and Newcombe 1982). Diurnal variations for a well-shaded coastal Oregon stream were less than 1°C, even during the day of the annual maximum (Brown and Krygier 1970). Streams bordered with relatively low densities of forest vegetation or which have a significant number of natural openings along the channel would be expected to have higher diurnal variations.

A time series of monthly average water temperatures extending from 1923 to 1975 has been reconstructed for Carnation Creek, B.C., using fifty-two years of air temperature records from a nearby permanent weather station (Estevan Point, B.C.) and a regression of air and stream temperatures for the period 1971 to 1984. A temperature record of this duration provides an estimate of the extent to which climatic variability has influenced undisturbed stream temperatures in that region. Historical variability in Carnation Creek stream temperatures has been relatively small. For all months of the year, the average monthly temperature lies within 1°C of the long-term monthly median at least 50% of the time.

Forest streams change temperature in space as well as time, again in response to energy transfers. As stream order increases, so usually does stream width, stream discharge, and the number of tributaries. As width increases, surface area exposed to solar radiation usually increases, because riparian vegetation may shade less and less of the stream surface. On the other hand, discharge also increases in a downstream direction. The balance between these factors ultimately determines the rate of temperature change downstream, especially in summer. For instance, in the tributaries of Carnation Creek, B.C., diurnal ranges during the summer increase in proportion to drainage area and stream width (both correlates of stream surface area), indicating the overriding importance of direct solar radiation during

periods of low discharge indicating the temperature regimes of small streams. During the winter there is no relation between stream surface area and diurnal range; and other factors, principally discharge and elevation, become important determinants of diurnal variation. In large rivers, diurnal temperature fluctuations are generally dampened because of the relatively large volumes of water contained by these systems (Hynes 1970).

Where tributaries join, or enter a main stream, the mixed temperature is the simple resultant of their individual temperatures, weighted by their respective discharges (Brown 1983). Thus a small tributary will produce little change in the temperature of a larger stream unless the small stream's temperature is greatly different. Hence, as stream order increases, the impact on temperature of tributaries entering the main channel generally decreases.

Because much of their flow is derived from forested headwater catchments, rivers in the Pacific Northwest exhibit seasonal temperature patterns similar to those of small forest streams. In Figure 3, average monthly temperatures are illustrated for three rivers across Oregon. Winter temperatures for the Nestucca River in the Oregon Coast Range are similar to those for the smaller Flynn Creek watershed shown in Figure 2. This similarity is primarily a consequence of the combined low net radiation inputs and high streamflows common at that time of year. In summer, monthly temperatures for the Nestucca River average approximately 18°C, or nearly 5 to 6°C warmer than those for the smaller Flynn Creek watershed. These downstream increases in monthly water temperatures during the summer occur primarily from net radiation inputs to the water as it flows through increasingly wider reaches of the stream system. In addition, flows are low at this time of year and serve to magnify the effects of energy inputs.

Winter temperatures for the Nestucca River in the Oregon Coast Range tend to be higher than for Fall Creek and the Umatilla River, located farther east (Figure 3). Fall Creek drains a portion of the western Cascades; the Umatilla River has its headwaters in the Wallowa Mountains of eastern Oregon.

The range of temperatures experienced in coastal streams is relatively low because of the maritime influence of the Pacific Ocean on the coastal climate. Lower winter temperatures occur for rivers draining the Cascades and mountain ranges farther east, where cold water temperatures associated with rainfall or snowmelt and cold nighttime air temperatures (which promote radiational cooling of stream water) are conducive to lower stream temperatures. Monthly temperatures in January for the Umatilla River in eastern Oregon average more than 3°C lower than those of the Nestucca River in the Oregon Coast Range. Downstream changes in water temperature, as water moves from headwater channels toward the mouth of a river system, are also described by Theurer et al. (1985).

Even though general temperature patterns are evident in forest streams, local anomalies may occur. Thermal stratification, while common in lakes, is generally precluded in streams, because of constant
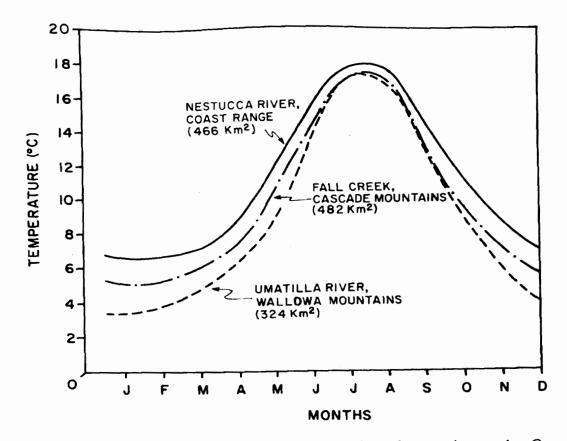
Figure 3.   Seasonal temperature patterns for three rivers in Oregon (1965-71).

turbulence of flowing water. However, several studies have shown that water near the bottom of pools is sometimes 5 to 10°C cooler than water near the surface (Keller and Hofstra 1982, Bilby 1984, Keller et al., in press). Cool-water sources usually result from a tributary stream, groundwater, or an upwelling of stream water that has been cooled by flowing through the streambed (Figure 4). The occurrence of these sources seems to be rare, accounting for only 1.6% of the stream surface area of a western Washington stream (Bilby 1984). Where relatively cool water enters a channel, fish and other organisms may find local thermal environments more favorable than surface water temperatures would indicate (Gibson 1966, Keller and Hofstra 1982); however, reduced dissolved oxygen levels associated with cool-water sources may limit their immediate usefulness to instream biota (Figure 5). The occurrence of such phenomena serves as a reminder that generalizations about the thermal environments of forest streams may be misleading.

In summary, the seasonal cycles in the temperatures of streams draining forested watersheds in the Pacific Northwest can be defined on temporal and spatial scales. There are clear seasonal patterns, with low levels of between-year variability. Diurnal variations also follow a predictable pattern and are generally very small. Spatially, there are regular, predictable effects of such variables as latitude, proximity to the ocean, and stream order. Particularly during summer months, however, there appears to be a significant amount of fine-scale heterogeneity
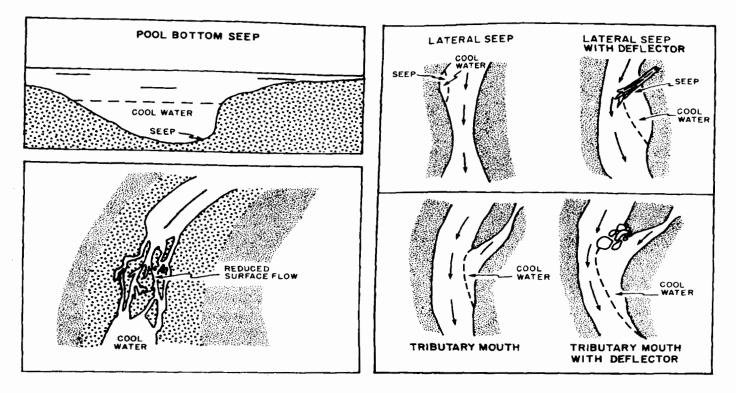
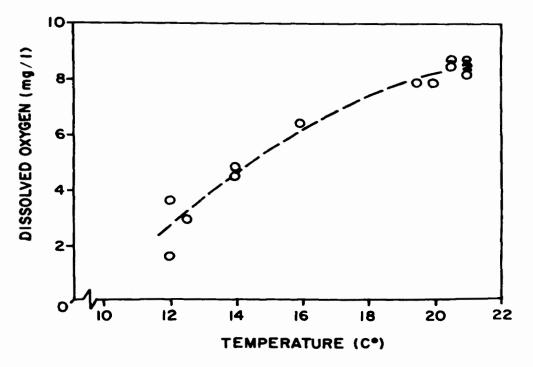Figure 4.   Examples of cool-water sources in mountain streams (from Bilby 1984).

Figure 5.   Relation between stream temperature and dissolved oxygen associated with a cool-water source in Redwood Creek, California (from Keller and Hofstra 1982).

in the thermal environment of streams brought about by variations in exposure to solar radiation, flow, channel widths, and the occurrence of cool-water upwelling. Nevertheless, the general temperature patterns represent a characteristic of the aquatic habitat that fish and other organisms must withstand and, perhaps more important, to which they have adapted their life strategies.

EFFECTS OF CANOPY COVER ON STREAM TEMPERATURES

Most stream temperature concerns in forest ecosystems have focused on summertime increases associated with forest harvesting. The energy balance components described earlier also operate for streams from which the canopy is removed. Again, the principal source of energy for heating small streams during summer conditions is incoming solar energy striking the water surface. The more canopy removed, the greater is the exposure of the stream to this heat source. Most of this incoming energy is stored in the stream, and its temperature rises accordingly.

Compared with solar radiation inputs, energy transfers involving convection or evaporation are of much less importance to the thermal regime of exposed mountain streams. Both require wind movement at the stream surface to be effective, in addition to temperature and vapor pressure gradients. Because of normally low wind velocities immediately above the water surface, neither process plays a significant role in controlling the temperature of an exposed stream (Brown 1983). Furthermore, these two processes tend to counterbalance each other. For example, if relatively warm air is present over a stream surface, the heat gain to the stream by convection will tend to be offset by heat loss through evaporation. This is important for several reasons. First, high air temperatures do not cause stream temperature to increase following canopy removal even though daily maximum air temperatures are usually at their highest during clear sunny weather, just as temperatures of streams are. However, the two variables are often highly correlated. Second, once a stream's temperature is increased, the heat is not readily dissipated to the atmosphere as it flows through a shaded reach. Hence, additional energy inputs to small streams can have an additive effect on downstream temperatures.

The net rate of heat exchange (N_h) per unit area of stream surface is shown in the following equation:

$$N_h = N_r + E + H + C \tag{1}$$

where N_r = net radiation

E = evaporation
H = convection
C = conduction

Although the net radiation term comprises both short- and long-wave components, the shortwave or incoming solar radiation portion is by far the most important factor that changes as a result of canopy reductions, particularly during the summer.

Seasonal and diurnal temperature patterns of exposed streams differ markedly from those of shaded, forest streams. For a channel with a forest canopy shading the water surface, the individual terms on the right-hand side of equation (1) remain relatively small over a 24-hour period, even in midsummer. Hence diurnal temperature fluctuations are also small. However, should the canopy be removed through harvesting activities or natural causes, the net heat gain or loss may be significantly altered.

During winter months, exposed streams may experience lower temperatures when there is no canopy to inhibit energy losses by evaporation, convection, or long-wave radiation from the stream. Long-wave losses are greatest when clear skies prevail, particularly at night. While this phenomenon is not important in coastal streams of Oregon and Washington, where nighttime cloud cover and relatively warm air temperatures are common, it may be important for streams at high elevations in the Cascades and streams farther east, or at northerly latitudes where snow accumulations are insufficient to cover and insulate the channel from energy losses. Because most research studies in the Pacific Northwest have concentrated on evaluating changes in summer stream temperatures, less is known about winter temperature changes, if any, as a result of reductions in canopy cover.

Studies in deciduous forest types of the eastern United States have found relatively small changes in winter stream temperatures due to forest harvesting. In Pennsylvania, changes in winter maximum temperatures ranged from -0.7 to +0.9°C; changes in winter minimums ranged from -1.4 to +1.0°C (Table 1). In West Virginia, complete removal of riparian trees lowered winter stream temperature minimums approximately 2°C (Lee and Samuel 1976). In New Jersey, dormant season stream temperatures remained unchanged following herbicide application to riparian forest vegetation. Results from studies of coastal streams in the Pacific Northwest (Brown and Krygier 1970, Holtby and Newcombe 1982) show little change in winter temperatures following canopy reductions from logging.

During the summer, the amount of direct solar radiation available to a stream whose canopy has been removed is substantial (Figure 6), hence exposed streams may experience large diurnal fluctuations. The extent to which the incoming solar energy increases the temperature of an exposed stream further depends on the surface area of the exposed reach and the stream discharge. Streams with small discharges and large exposed areas inevitably experience the greatest temperature increases (Sheridan and Bloom 1975).

Research associated with a variety of forest types and geographic locations has identified the magnitude of temperature increases to be expected from canopy removal. For summertime conditions in the eastern United States, increases in average maximum temperatures following reductions or removal of forest canopy have generally ranged from 3 to 10°C (Table 1). Minimum temperatures in summer either remained unchanged or were generally limited to increases of less than 1°C.

Table 1. Summary of temperature changes associated with forest management activities and experimental treatments on forest watersheds, eastern United States.

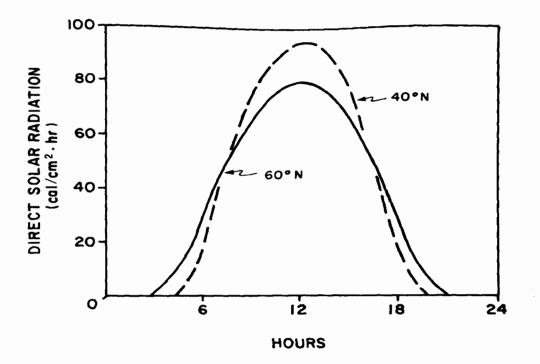| Location	Treatment	Stream Temperature Variables	Temperature Change (°C)	Reference
Georgia	Clearcut with partial buffer strip	Average June-July maximum	+6.7	Hewlett and Fortson (1982)
Maryland	Riparian harvest up to 40 m from channels	Average summer maximum Average summer minimum	+4.4 to 7.6 +0.6 to 1.1	Corbett and Spencer (1975)
New Jersey	Riparian herbicide application	Average summer maximum Average summer minimum Dormant season	+3.3 Unchanged Unchanged	Corbett and Heilman (1975)
North Carolina	Deadened cove vegetation	Average summer maximum	+2.2 to 2.8	Swift and Messer (1971)
	Complete clearcut	Average summer maximum	+2.8 to 3.3	Swift and Messer (1971)
	Understory cut	Average summer maximum	0 to 0.3	
Pennsylvania	Riparian harvest (lower third of slope)	Average summer maximum Average summer minimum	+3.9 Unchanged	Lynch et al. (1975)
	Clearcut with herbicide treatment	Average June-July maximum Average June-July minimum	+10 to 10.5 +1.7 to 1.8	Rishel et al. (1982)
		Average Dec.-Feb. maximum Average Dec.-Feb. minimum	-0.5 to +0.9 -1.4 to +0.2	Rishel et al. (1982)
	Commercial clearcut with buffer strip	Average June-July maximum Average June-July minimum	+0.6 to 1.6 0 to 0.6	Rishel et al. (1982)
		Average Dec.-Feb. maximum Average Dec.-Feb. minimum	-0.7 to +0.9 -0.5 to +1.0	Rishel et al. (1982)
West Virginia	Clearcut	Average summer maximum	+4.4	Kochenderfer and Aubertin (1975)

Figure 6. Daily pattern of potential direct-beam solar radiation at a stream surface during clear weather (assumed atmospheric transmission coefficient = 0.9) on June 22, for selected latitudes (Buffo et al. 1972).

For the Pacific Northwest, watershed studies in the Coast Range and the Cascade Mountains of Oregon have shown increases in mean monthly maximum temperatures of about 3 to 8°C (Table 2) following clearcut harvesting. Burning may add another 1°C increase. At Carnation Creek on Vancouver Island, British Columbia, Holtby and Newcombe (1982) found that summer temperature increases due to logging were proportional to the basin area logged. They predicted a 7°C increase in mean summertime water temperature if the entire watershed was clearcut. Studies in the Pacific Northwest also show that the minimum temperatures in summer are much less altered by canopy removal and are generally limited to increases of less than 1 or 2°C.

Concern over altered temperatures after logging streamside vegetation usually focuses on the inevitable increases in maximum temperatures observed during the summer. This focus is very much a result of the toxicological perspective on temperature changes that is prevalent in fisheries research. However, in the majority of cases in the Pacific Northwest, stream temperatures in deforested watersheds, while invariably warmer than they were in the forested state, do not approach the tolerance limits of the resident fish species.

Holtby (1986) compared temperature changes over three biologically interesting periods at Carnation Creek: (1) the winter (October through February), (2) the spring (April and May), and (3) the summer (May through September). Logging-related increases in temperature (as indexed by thermal summations), from 1977 to 1984, averaged 15% (range

Table 2. Summary of summer temperature changes associated with forest management activities on forest watersheds, Pacific Northwest.

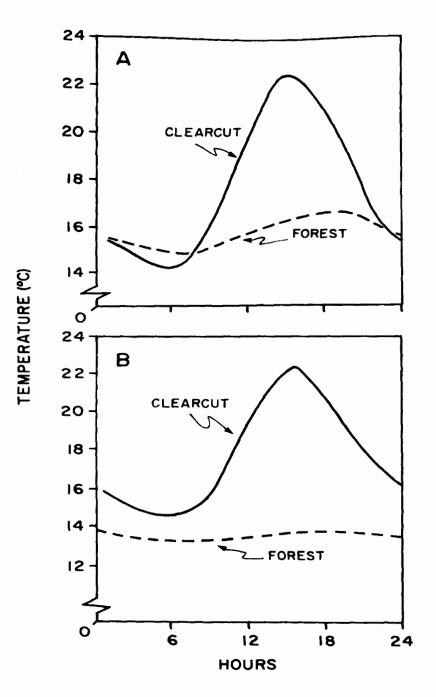| Location	Treatment	Stream Temperature Variables	Temperature Change (°C)	Reference
Alaska (Southeast)	Clearcut and natural openings	Δ Temperature per 100 m of channel	0.1 to 1.1°C/100 m Average = 0.7°C/100 m	Meehan (1970)
British Columbia (Vancouver Island)	Logged (Tributary H)	Average June-August diurnal temperature range	0.5° to 1.8°C increase over pre-treatment levels	Holtby and Newcombe (1982)
	Logged and burned (Tributary J)	Average June-August diurnal temperature range	0.7° to 3.2°C increase over pre-treatment levels	Holtby and Newcombe (1982)
Oregon (Cascades)	Clearcut	Average June-August maximum	4.4 to 6.7°C	Levno and Rothacher (1967)
	Clearcut and burning	Average June-August maximum	6.7 to 7.8°C	Levno and Rothacher (1969)
Oregon (Coast Range)	Clearcut	Average July-Sept. maximum	2.8 to 7.8°C	Brown and Krygier (1967)
	Clearcut and burning	Average July-August maximum	9 to 10°C	Brown and Krygier (1970)
Oregon (Cascades)	Mixed clearcut and forested reaches	Δ Temperature per 100 m of channel	0 to 0.7°C/100 m	Brown et al. (1971)
	Tractor striped area	Δ Temperature per 100 m of channel	15.8°C/100 m	Brown et al. (1971)

Figure 7. Summertime stream temperatures during clear weather in (A) West Virginia (from Lee 1980), and (B) Coast Range of Oregon (from Brown and Krygier 1967).

of 2 to 32%) during the winter, 27% (range of 18 to 36%) during the spring, and 37% (range of 16 to 56%) during the summer.

The increased exposure of small headwater streams draining clearcuts to incoming solar radiation leads to substantial increases in diurnal fluctuations (Figure 7). In some situations, the diurnal range in midsummer can increase by more than 15°C if the overstory shade is

completely removed (Brown and Krygier 1970, Moring 1975a). In other situations, increases in diurnal ranges have been considerably less. Increases in average diurnal ranges during summer after complete clearcutting along tributaries to Carnation Creek were less than 3°C (Holtby 1986). In the main creek, average diurnal range increased approximately 1°C during the summer. Increased diurnal ranges during most of the winter months were detectable but nevertheless were considerably smaller.

Because direct-beam solar radiation is the primary factor influencing temperature change in summer, the effect of partial canopy removal is directly proportional to the reduction in canopy providing shade to the stream. What this signifies is that leaving buffer strips represents an effective means of preventing temperature change for many mountain streams.

The importance of a buffer strip for preventing increases in stream temperature can be determined by measuring its angular canopy density (ACD). Whereas canopy density is usually expressed as a vertical projection of the canopy onto a horizontal surface, ACD is a projection of the canopy measured at the angle above the horizon at which direct-beam solar radiation passes through the canopy. This angle is determined by the position of the sun above the horizon during that portion of the day (usually between 10 a.m. and 2 p.m. in mid to late summer) during which solar heating of a stream is most significant. Thus ACD can provide a direct estimate of the shading effects of streamside vegetation. Although it is possible for natural forest vegetation to have ACDs of 100%, indicating complete shading from incoming solar radiation, the ACD of old-growth stands in western Oregon generally falls between 80 and 90% (Brazier and Brown 1973, Steinblums et al. 1984). In northern California, Erman et al. (1977) found ACDs to average 75% along undisturbed streams.

The relative degree of shading provided by a buffer strip depends on a range of factors (e.g., species composition, age of stand, density of vegetation). Although buffer-strip width is also important, by itself it is not generally a good predictor of shade protection. Figure 8 illustrates the variability of ACD associated with buffer-strip width for forest stands in the Coast Range and Cascade Mountains of Oregon. Buffer strips with widths of 30 m or more generally provide the same level of shading as that of an old-growth stand.

How can we predict the effect of complete removal of riparian vegetation, partial removal, or a buffer strip on the daily temperature pattern of a stream? The answer is relatively simple: by determining the change in energy available to the stream surface. In summer this means determining how much additional surface will be exposed to direct sunlight during clear weather. This task is comparatively easy when attempting to predict the effect of completely exposing a stream reach that was fully shaded. It is more difficult to predict the change in exposed surface area that will occur following partial removal of the canopy.
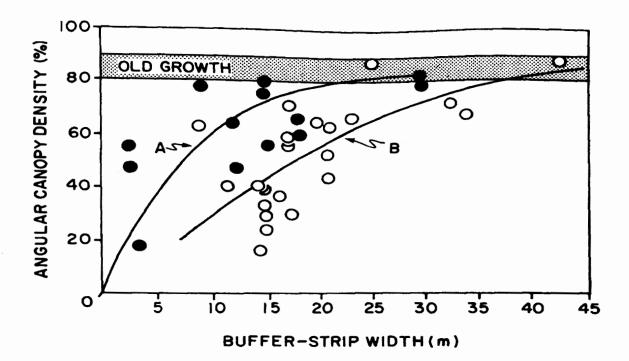
Figure 8.   Relation between angular canopy density (ACD) and bufferstrip width in western Oregon. Data for (A) from Brazier and Brown (1973); data for (B) from Steinblums et al. (1984).

Once the surface area A exposed to direct-beam radiation is estimated, the increase in net energy N_h (mostly shortwave solar radiation) can be readily determined from tables and combined with an estimate of stream discharge Q to predict the temperature increase ΔT produced by harvesting:

$$\Delta T = \frac{N_h \times A}{Q} \times 0.000167 \qquad (2)$$

where N_h = net rate of heat added to the stream ($cal/cm^2 \cdot min$)

   A = surface area of stream exposed to incoming solar radiation (m^2)
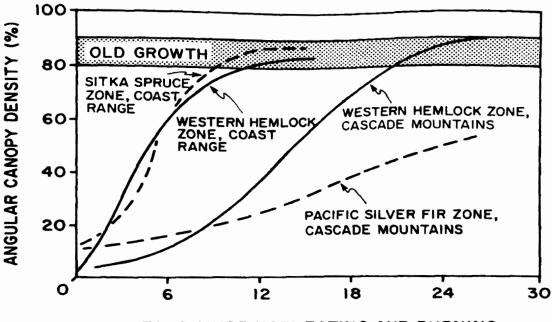
   Q = streamflow (m^3/sec)

A detailed description of this predictive technique and the methods for laying out buffer strips to ensure temperature control are given by Currier and Hughes (1980) and Brown (1983).

Equation (2) works well for predicting temperature increases from harvest along short reaches of stream where incident solar radiation is the major contributor to the energy balance. On reaches greater than 1,000 meters, evaporative and conductive energy transfers begin to become significant dissipators of energy and must be accounted for in the prediction. Similarly, the temperature and inflow rate of ground-water must be quantified. These variables add a great deal of

complexity to the prediction (Beschta 1984), making it no longer a simple, easy-to-apply technique. From a practical standpoint, this situation also means that streams exposed over long reaches will not continue heating indefinitely (e.g., Theurer et al. 1985). They will eventually reach an equilibrium temperature as evaporation, convection, conduction, and groundwater inflow balance the incoming radiation load.

What happens to temperature when streams flow from a fully exposed reach into a shaded reach? Will they cool down just as they warmed in the sun? Probably not unless cooler water from a tributary or from subsurface seepage enters the channel. Even though the direct solar radiation may be greatly reduced in the shady reach, it is still greater than long-wave radiation losses from the warm water and is likely to be greater than energy losses from evaporation, convection, or conduction. Thus the water temperature will remain relatively unchanged in the shaded reach unless it mixes with other cooler water within the reach. Management strategies to prevent excessive temperature increases by alternating shaded with unshaded reaches will be effective only if cooler inflows occur within the shaded reaches. Where cooler inflows do not occur, temperature increases from each exposed reach will not decrease appreciably through the shaded reaches, and the result is a "stair-step" temperature increase in the downstream direction (Brown et al. 1971).

Because heat added to a stream is not readily dissipated, temperature increases in small headwater streams can increase the temperature regimes of downstream reaches. The magnitude of downstream effect depends on the relative increase in temperature and amount of streamflow from the exposed tributaries. The mixing of any heated water, from exposed headwater streams, with cooler subsurface seepage or at tributary junctions will moderate the pronounced diurnal temperature increases experienced in an exposed headwater stream. Nevertheless, where extensive reaches of channel have become exposed either as a result of clearcut logging without buffer strips or from sluiced channels due to mass soil failures and debris torrents, a cumulative effect on the downstream thermal regime should be expected. Unpublished data (Beschta and Taylor 1986) for Salmon Creek, a 325 square kilometer drainage in the Oregon Cascades, shows such a cumulative effect. A thirty-year trend of increasing summer stream temperatures has been measured during a period of extensive logging and roading throughout the basin. During the summer, maximum stream temperatures at the mouth of this drainage have increased from 16°C in the mid-1950s to 22°C in the late 1970s; minimum temperatures in summer increased approximately 2°C (from 12 to 14°C) during this same period.

Increased temperatures have also been observed in the Middle Santiam River of the Oregon Cascades as the basin was logged. Logging activities in this basin have been largely limited to areas along the lower 11 km of the river, with areas farther upstream essentially undisturbed. Thus temperature changes downstream of the logged area can be referenced against temperatures of the undisturbed section. Average daily maximum temperatures for the period May to October increased approximately 1°C from 1972 to 1982, apparently as a result

Figure 9. Relation between angular canopy density (ACD) and stand age for vegetation zones in western Oregon (Summers 1983).

of harvest (K. Sullivan, Weyerhaeuser Company, Tacoma, pers. comm.).

When temperature increases are produced by complete or partial exposure of a stream, they will subsequently decline as riparian vegetation returns. The rate of shade recovery depends on streamside conditions and vegetation. Sites in moist coastal ecosystems of the Pacific Northwest recover more rapidly than those in more arid ecosystems; sites at lower elevations more rapidly than those at higher elevations. In western Oregon, Summers (1983) examined sites with small streams that had been clearcut and burned at various times in the past to evaluate the recovery of shade (Figure 9). On the average, 50% of a stream was shaded within about five years of harvesting and burning in the Coast Range, within fifteen years from lower elevations of the Cascades (Western Hemlock Zone), and within twenty-five years for the higher elevations of the Cascades (Pacific Silver Fir Zone). Whereas small streams may be quickly overtopped by brush and effectively shaded from direct-beam solar radiation, larger streams, which require the canopies of tall conifers for shade protection, require longer periods.

Several alternatives are generally available to forest managers to prevent excessive temperature changes in order to avoid potential conflicts with fisheries interests, water quality changes, or other concerns. Where no change in temperature is permitted, a buffer strip is the obvious solution. But where some change in temperature is acceptable following logging, small clearcuts along streams, partial cuts or partial cuts within buffer strips (leaving only that vegetation that

provides shade during a critical time of the year), scheduling of cutting activity over time in a drainage, or some combination of these methods can provide a desired level of temperature protection.

THERMAL EFFECTS ON THE STREAM ECOSYSTEM

Research on the effects of thermal alterations on fish communities falls into three general areas that serve as foci for our discussion: (1) trophic effects (effects of thermal alteration on other components of the community that affect fish), (2) thermal tolerances and preferences of fishes, and (3) fish metabolism, development, and activity.

Trophic Effects

Water temperature changes in mountain streams may not only influence fish populations and productivity but also that of the microbial community, algae, and invertebrates. These latter biotic components form the energy base for fish communities, and changes in these compoents can potentially be translated into impacts on fish through a change in available food. The energy base for stream biota comes primarily from two sources: algal production and terrestrial sources of organic matter (needles, leaves, twigs, etc.) (Fisher and Likens 1973). In most forest streams, the largest proportion of available energy is from terrestrial organic inputs. The nutritional value of this organic matter to animals that ingest it is due largely to an encrusting layer of microorganisms that develops after entry into the stream (Kaushik and Hynes 1971). With increased temperatures, these microflora develop more rapidly and utilize available organic matter at a higher rate (Suberkropp et al. 1975). Rapid decomposition of organic material may promote increased invertebrate production more quickly than in cooler streams, thus leading to additional fish food at an earlier time. However, the organic matter would thus be consumed over a shorter period, so this effect may be transitory.

Where streamside vegetation has been removed, light availability and stream temperatures typically increase. Although Murphy et al. (1981) demonstrated increased stream primary production mainly from increased light availability after canopy removal, it is difficult to separate the influence of light and temperature. Light limitation of aquatic plant production has been demonstrated in several Pacific Northwest streams (Stockner and Shortreed 1978, Rounick and Gregory 1981, Walter 1984). Both increased light and temperature generally cause higher production of stream algae and, in many cases, a change in species composition. Phinney and McIntire (1965) examined the influence of both light and temperature on production of a natural assemblage of periphyton in an artificial stream channel. They found that algae production was higher at 18°C than it was at 8-10°C for all tested light levels. However, the influence of increased light on algae growth in the two channels differed. At 18°C, algal production increased with light intensity up to an intermediate level and decreased at higher illumination. In the cooler channel, algal productivity increased up to the highest light level tested. Kevern and Ball (1965) and Bisson and Davis (1976) also noted a marked increase in periphyton

production in heated stream channels compared with channels exposed to similar light regimes at lower temperatures. In contrast, Stockner and Shortreed (1978) conclude that nutrients and light are important regulators of algal growth in Carnation Creek, B.C., but that temperature does not have an important regulatory effect.

Changes in the taxonomic composition of the algal community in a stream following exposure to direct sunlight have been noted in several studies. In a spring-fed stream where temperature was constant (7°C), but light was experimentally varied through shade manipulation, Busch (1978) found that increased light both altered the species of algae present and caused an increase in algal biomass and invertebrate production. Warren et al. (1960) noted that in Oregon streams filamentous green algae dominated where at least 3% of full sunlight reached the substrate. In shaded stretches, diatoms predominated. Temperature also probably plays a role in this shift from a flora dominated by diatoms to one of green algae. Bisson and Davis (1976) noted a heavy growth of filamentous green algae in their heated channel. Their control channel had far less of this type of algae despite being exposed to similar light levels. The heavy growth of filamentous algae in the heated stream trapped considerable amounts of fine sediment, resulting in a shift in the invertebrate community to one dominated by oligochaete worms. These worms were rarely consumed by fish during this experiment. However, the general significance of such shifts in algal community composition on fish production in mountain streams is not well understood.

The influence of the changes in the energy base on higher tropic levels of the stream after canopy removal is difficult to interpret (Lee and Samuel 1976). Higher production levels of both microorganisms and algae suggest corresponding increases at higher levels of the food chain. However, the faster processing rate of organic matter by microbes coupled with a decrease in the input of leaves, needles, and other organic materials after clearcutting may lead to a scarcity of this material at certain times of the year. For example, Fisher and Likens (1973) found that under natural forested conditions, organic matter of leaf and twig size persisted in a small New England stream for about a year. With the more rapid processing at higher temperature, the residence time of this material in the stream should decrease. Since most terrestrial organic matter enters the stream as a pulse in autumn, an increased rate of processing could reduce summer stocks of this material, hence lowering food supplies for invertebrates dependent on this material. Thus when streams become exposed following removal of riparian vegetation, a short-term increase (from logging slash) followed by a longer term decrease in the availability of terrestrial organic matter may occur. The effect on the invertebrate populations and the extent to which it is offset by greater algal productivity are not known.

Nevertheless, despite the potential for deleterious effects, invertebrate standing crops in headwater streams that drain clearcuts are generally greater than those either in old-growth forests or in second-growth deciduous forests (Hughs 1966, Newbold et al. 1980, Smith 1980, Murphy and Hall 1981, Murphy et al. 1981). It would

appear that the possible deleterious effects of removing riparian vegetation are outweighed by the increased primary production resulting from increased temperatures, light levels, and nutrients.

Invertebrates may be directly influenced by temperature increases, apart from the influence of their food supply. At higher temperatures, invertebrates feed more actively and, as a result, exhibit elevated growth rates (Cummins et al. 1973).

Temperature increases have at times been related to noticeable decreases in invertebrate production. Minshall (1968), studying a spring-fed brook in Kentucky, found a large decrease in both species diversity and numbers of individuals when stream temperature was elevated in a clearcut. However, spring-fed streams, in general, tend to have a constant, cold temperature year round and hence a fauna specialized for these unusual circumstances. This type of system may be especially sensitive to elevated temperatures.

Higher stream temperatures can also cause accelerated development of aquatic insect larvae, leading to early adult emergence (Nebeker 1971a, 1971b, Moore 1980). Salmonid fishes prey heavily on emerging adults, and accelerated insect development may benefit fish by making more food available earlier in the year. However, for most trouts (Salmo spp.) the emergence of fry from spawning gravel and the onset of active feeding coincides with spring and early summer hatches of aquatic insects.

Bisson and Davis (1976), working with two experimental stream channels, one heated about 4°C over the other, reported a reduction in the number of taxa in the heated channel. They also reported that nearly all the species represented in the channels produced higher biomasses in the control stream. There were exceptions to this rule, however, the most notable being a species of oligochaete worm and a snail, both of which exhibited increased production in the channel. Neither species was eaten by the juvenile chinook salmon in the channels, and as a result the increased production was of no benefit to the fish.

Sherberger et al. (1977) indicate that a temperature of at least 28°C was needed to influence mortality in Isonychia, a mayfly, while Hydropsyche, a caddisfly, withstood brief exposures up to temperatures of 26.5°C. Temperatures below the lethal limit did not have an effect on survival. At least in the case of these two invertebrates, lethal levels are above that needed to severely affect salmonids. Thus increased temperatures would probably eliminate the fish before their food resource was affected.

Some invertebrates are able to avoid high summer temperatures, such as those created by canopy removal, by adjusting their life cycle to spend the stressful period in a resistant, resting stage. Macan (1961) demonstrated that the mayfly, Rithrogena semicolorata, emerged earlier in the year in a warm stream than normally seen in cooler waters. The eggs deposited by the adults in spring in the warmed stream remained dormant for a longer period than those in cooler streams,

hatching only when water temperatures decreased in autumn. Many invertebrates, however, such as those that spend one or more years in a larval form, would not generally be able to avoid temperature extremes by using this tactic.

Increased temperatures have been implicated in several studies as leading to increased entry of invertebrates into the drift (Pearson and Franklin 1968, Waters 1968, Bisson and Davis 1976). However, other investigators have not found this phenomenon (Bishop and Hynes 1969, Wojtalik and Waters 1970, Reisen and Prins 1972). The drift reaction of various invertebrates is probably species specific, which would account for the discrepancies noted in these studies. Increased drift rate would make more food available for fish, since drift forms the major food source for salmonids.

The influence of elevated temperatures on salmonid production of natural systems is difficult to delineate because of the variety of other factors concurrently affected. However, more abundant invertebrates have been observed in streams draining clearcuts (e.g., Murphy et al. 1981). Increased algal productivity leading to higher invertebrate production, and consequently to elevated food availability for fish, has been hypothesized as a cause of the frequent observation of increased salmonid production in streams exposed to sunlight (Murphy and Hall 1981, Weber 1981, Hawkins et al. 1983, Bisson and Sedell 1984). The consistency of these observations has led to general acceptance of the hypothesis that salmonid abundance is greater in streams draining clearcuts because there is more available food. Consequently, it is also generally accepted that an understanding of the effects of logging on the entire stream ecosystem is essential if we are to make progress in understanding the narrower problem of logging impacts on fish production.

Thermal Tolerances and Preferences of Fishes

The systematic study of the thermal tolerances and preferences of fishes began in the last century (see Brett 1970). Our understanding has slowly broadened from the concept of a single end point (e.g., a single upper lethal temperature) to a two or three factor concept (the zone of thermal tolerance of Fry 1964, where lethal temperatures are modified by acclimation temperature and exposure) and finally to a multifactorial concept where a multidimensional zone of thermal tolerance is defined by many interacting environmental factors (Brett 1970). Such studies are of necessity conducted under the tightly controlled conditions of the laboratory. The relevant objective of this work is to define for a particular species the boundaries of the thermal habitat. It may then be inferred that any land use activity that drives temperatures outside these boundaries will have deleterious and possibly lethal consequences.

Have any generalities relevant to our general topic emerged from this work? Apparently salmonids are tolerant of the extremes in temperature they are likely to encounter over their life spans and geographic ranges. In particular, the life stages of salmonid species that rear in freshwater seem especially tolerant of extreme high

temperatures (extreme in the sense that most species can tolerate temperatures that are many degrees higher than any they are likely to encounter).

Because fish are cold-blooded, or poikilothermic, the temperature of their external environment dictates their internal temperature, which in turn regulates metabolic rate. Thus changes in water temperature directly influence the physiology and activity of fish. Furthermore, the relative sensitivity of fish to temperature changes depends, to a great extent, on their stage of development.

Early studies evaluated the effects of elevated temperatures on the survival of salmon eggs. For example, Combs and Burrows (1957) examined the influence of various temperatures on the survival of chinook salmon eggs. They found the upper lethal limit to be between 14 and 15.5°C. Similarly, Seymour (1959) reported that chinook eggs would not survive to the stage of vertebral development at temperatures in excess of 16.5°C. Sockeye salmon eggs appear to be even more susceptible to elevated temperatures, as Combs (1965) set the lethal level for development of this species at 13.5°C. Even in cases where temperature elevation is not sufficient to cause direct egg mortality, morphological characteristics of the fish can be altered as a result of high temperature during embryonic development (Orska 1963). Although laboratory studies provide an upper bound on temperature tolerance of eggs and embryos exposed to constant temperatures, the temperature environment in redds may be quite different.

Spawning and egg development in salmonids occurs during the autumn, winter, and spring. In coastal Oregon, Ringler and Hall (1975) found intragravel water temperatures during the time of coho salmon egg incubation in a stream draining a clearcut watershed to be well below those reported to cause developmental abnormalities. In the case of some races of spring-spawning salmonids, egg development may continue into late spring when the possibility of coincident low stream flow and sunny days could produce water temperatures detrimental to the development of the eggs. The extent to which this occurs is unknown. In addition to the influence elevated temperatures may have on egg development, depressed temperatures have been seen to lengthen incubation periods or increase freezing mortalities (Alderdice and Velsen 1978, Reiser and Wesche 1979, Reiser and White 1981). However, the effect removal of streamside vegetation has on minimum stream and intergravel temperatures in winter has generally received little attention (Needham and Jones 1959, Sheridan 1961).

Lethal threshold temperatures for Pacific salmon and steelhead trout have been identified for laboratory conditions (Figure 10), where the fish are held at a given temperature for long periods of time. This situation does not exist under natural conditions (even where temperatures have been elevated because of the removal of streamside vegetation), hence the direct application of laboratory temperature limits to field conditions is tenuous. Streams flowing through clearcut areas may display sizable fluctuations of water temperature over the period of a day, and maximum temperatures may exceed the reported lethal threshold temperatures for a brief time. However, these streams may
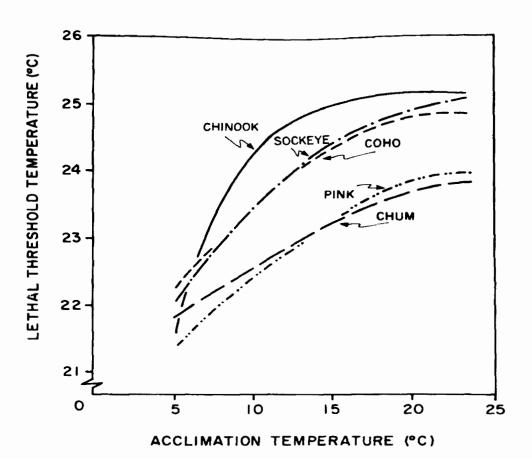
Figure 10. Lethal threshold temperatures for juvenile salmonids (from EPA 1973): chum salmon (Oncorhynchus keta), pink salmon (O. gorbuscha), coho salmon (O. kisutch), sockeye salmon (O. nerka), and chinook salmon (O. tshawytscha).

contain sizable populations of salmonids (Bisson et al. 1985). Apparently fish are able to withstand periodic, short-term exposures to fairly high temperatures with minimal detrimental impact.

The temperature levels preferred by rearing juvenile salmonids have also been evaluated in a number of laboratory studies. Brett (1952) found that the range of greatest preference by all species of Pacific salmon was from 12 to 14°C for acclimation temperatures ranging from 5 to 24°C. Brett (1952) also noted a definite avoidance of water over 15°C. Mantelman (1960) observed that juvenile rainbow trout were most commonly found in water ranging from 13 to 19°C and actively avoid water in excess of 22°C. These preferred temperatures may be exceeded in streams draining clearcut watersheds (Brown and Krygier 1970, Sheridan and Bloom 1975).

Elevated temperatures can also influence salmonid behavior. Upstream movement of adult sockeye salmon and steelhead trout was curtailed in the Columbia River when water temperatures reached 21°C (Lantz 1971). At these times the migrating fish congregated in the mouths of cooler tributaries until water temperatures decreased. Keenleyside and Hoar (1954) reported that both chum and coho salmon

fry exhibited progressively increased rates of downstream migration as water temperature increased. Temperature preferences of fish have been the target of many studies; these have been summarized by Coutant (1977) and Jobling (1981).

For the coho salmon of Carnation Creek there is no evidence that increased summer temperatures (several degrees outside of their probable historical limits) and increased diurnal fluctuations affected fish distributions, at least on a macroscale. The availability of small-scale cover ("fine logging debris") was the important factor in determining the abundance of fry in stream sections whose banks had been completely clearcut, not the increases in stream temperatures in those sections (Scrivener and Andersen 1984).

Larkin (1956) noted that, as a rule, freshwater fish are adaptable to a wide range of environmental conditions and that the outcome of competitive interactions may vary depending on these conditions. A species that is dominant under one set of conditions may not necessarily prevail when conditions differ. Two recent studies have examined the influence of water temperature on interspecific interactions between fish. Reeves (1985) showed that the outcome of interactions between juvenile steelhead trout (age 1+) and the redside shiner (Richardsonius balteatus) was mediated by water temperatures. Water temperatures and the presence of the other species influenced production and activity in laboratory streams and distribution in the field and laboratory. Trout dominated in cool water (12 to 15°C) and shiners in warm water (19 to 22°). Baltz et al. (1982) found that competition between two species of nongame fish was affected by water temperature: one species dominated in cool water and the other in warm. Alteration of the temperature regime may influence not only growth and survival of a given species but also the structure of the fish community.

The development of thermal tolerance criteria in laboratory studies seems to have been markedly unsuccessful in helping understand the effects of logging on fish communities in the Pacific Northwest. To our knowledge, there are no records of elevated temperatures following shade removal that have led to extensive fish kills. An exception is the fish kill observed following a hot slash fire in Needle Branch, Oregon, during the Alsea Watershed Study (J. D. Hall, Oregon State University, Corvallis, pers. comm.). In fact, there is a general tendency for salmonid biomass to be higher in streams draining clearcuts (Burns 1972, Smith 1980, Martin et al. 1981, Murphy and Hall 1981, Holtby and Hartman 1982, Hawkins et al. 1983, Bisson and Sedell 1984, Scrivener and Andersen 1984). While such increases may have been due to many factors, the generality of the observation suggests that temperature increases resulting from clearcut logging do not, by themselves, have significant deleterious effects on salmonid abundance. One reason is that stream temperatures throughout the region seldom exceed, for extended periods, the tolerance limits of the resident salmonid species. The fish themselves also appear to be behaviorally "plastic" and can act to reduce either or both the temperatures they are exposed to and the duration of the exposure. For instance, salmonids appear to seek out cool water regions in streams where temperatures approach and exceed tolerance limits (Gibson 1966, Kaya et al. 1977). Even in studies where

elevated summer temperatures, resulting from streamside disturbance, appear to have precluded salmonids, strong arguments can be made that the temperature effects were indirect. For example, Barton et al. (1985) concluded that the suitability of streams in southern Ontario for trout was characterized by maximum summer temperatures. While the effects of temperatures could have been direct, the authors suggest that elevated temperatures over several decades allowed the successful invasion of warm water competitors of the salmonids, possibly result- ing in their competitive exclusion.

Although salmonid populations may respond favorably to opening of the riparian canopy, increased water temperatures, or both, resulting from management activities in these streams, the cumulative effect of these changes on other areas of the watershed has received little or no consideration in the Pacific Northwest. Water temperature in mid-order streams lower in a watershed depends largely on the temperature of water entering from upstream. Mid-order streams are important rearing areas for juvenile anadromous salmonids, especially chinook salmon and >1+ steelhead trout. They also have a more diverse fish community than lower order streams do (Vannote et al. 1980). Changes in environmental conditions may result in a decrease in available habitat for salmonids and alter the outcome of interactions between salmonids and potential competitors. Environmental changes less favorable to salmonids, such as increased water temperature in higher order streams, could offset any increase in abundance or production of anadromous salmonids that might occur from opening the canopy along lower order streams, or could even result in an overall decrease in population.

Temperature Effects on Fish Metabolism, Development, and Activity

The second general approach that has been used to study the effects of thermal change of stream fishes considers the effects of temperatures on metabolism, development, and activity. Within the bounds of thermal tolerance for any species, temperature is an im- portant modifier of metabolism which then acts through numerous path- ways to affect development, growth, activity, and reproduction or, more generally, survival and success (Brett 1958, Brett 1970, Lantz 1971). This rather broad field has been reviewed extensively (e.g., Fry 1967, Warren and Davis 1967, Brett 1970).

Except when fish are starving, the response of growth and activity to increasing temperatures is enhancement up to some optimum temperature and them diminution as the optimum is exceeded. In gen- eral, the optimal temperatures for growth and activity are similar to those likely to be encountered at a particular stage of the fish. It is also generally the case that the optima are rather broad, especially for species and life stages where the temperatures encountered are wide ranging.

Laboratory studies with salmon and trout at constant temperature levels have generally shown decreased growth with higher temperatures when food was limiting. A fish will not grow until metabolic energy requirements are first met (Warren and Davis 1967), and the metabolic rate increases with temperature. Dwyer and Kramer (1975) examined the

metabolic rate of cutthroat trout at several temperatures. They measured the lowest metabolic rate at 5°C and the highest at 15°C with a decrease in rate at 20 to 24°C. Normally, metabolic rate would be expected to continue to increase as a function of temperature; however, in this experiment the trout held at 20 and 24°C fed very little, and it is likely that the decrease in metabolic rate was brought on by starvation. Wurtsbaugh and Davis (1977) found that maintenance food levels (the amount needed to maintain constant body weight) for rainbow trout were 2.7% of body weight per day at 6.9°C and 7.5% at 22.5°C. Averett (1968) found that juvenile coho salmon required twice the amount of food to grow at 17°C than at 5°C. In many salmonids, however, the dimunution in growth and swimming performance with increasing temperature occurs primarily at temperatures near the lethal thresholds (e.g., Brett 1967, Brett et al. 1969).

Wurtsbaugh and Davis (1977) indicated that if steelhead trout were fed limited amounts of food, growth decreased at higher temperatures. The difference in productivity lessened, however, if the ration was increased. Similarly, the production of coho salmon has been shown to decrease at higher temperatures under conditions of limited food (Iversen 1972). The decreased production in Iversen's (1972) study was attributed to both increased metabolic rate and a reduction in food availability due to a decrease in the invertebrate population in the artificial stream channel in which the experiment was conducted. Bisson and Davis (1976) also reported a decrease in fish production with increased temperature for juvenile chinook salmon. They subjected artificial stream channels to diurnal and annual temperature cycles with one of the channels heated and maintained at a temperature approximately 4°C higher than the control. Production in the cooler channel exceeded that in the heated channel by 100% the first year of the experiment and 30% by the second year. The decreased production in the heated channel was attributed to increased metabolic requirements and reduced food levels.

Fish productivity at elevated temperatures could probably be maintained, provided the food supply increased enough to compensate for increased metabolic requirements. In a study in which water temperature in artificial streams varied daily, production of juvenile steelhead trout (>1+) was two and one half times greater in cooler water (12 to 15°C) than in warmer (19 to 22°C) water (Reeves 1985). One reason for these differences was that fish in the cooler water were able to maintain territories in areas of higher food concentration, which were in areas of greater water turbulence.

Nearly all these studies on the influence of temperature on fish production were conducted in artificial streams. More recent studies of natural streams have not always corroborated the results from artificial channels. Martin et al. (1981) compared a population of cutthroat trout inhabiting a shaded section of stream with fish in a section of stream exposed to direct sunlight. They could find no difference in trout biomass or density between the two sections, although the exposed section had a daily maximum temperature that averaged 2°C higher than the shaded section. However, in a final analysis of the data set, Martin (1985) concluded that in the canopy area with no temperature change,

density increased. In the open area where temperature increased, growth increased but density did not. Some studies of salmonid populations in streams exposed to sunlight have reported increases in production. For example, Murphy and Hall (1981) reported higher salmonid biomass in streams exposed to sunlight than in streams flowing through old-growth forest in Oregon. The temperature increases in the exposed streams were slight, ranging from 0.1 to 1°C, thus the fish biomass increase is probably attributable to factors other than increased temperature. Bisson and Sedell (1984) also reported higher salmonid biomass in streams draining clearcut areas than in shaded systems in southwestern Washington, but these authors did not monitor stream temperatures.

While the growth efficiency of salmonids is theoretically highest at low temperatures, activity of fish in cold water is at a minimum and feeding rates are correspondingly depressed. Thus optimum growth usually occurs at some intermediate temperature where activity levels are high enough to ensure active feeding, and metabolic conversion efficiencies are also relatively high. "Optimum" stream temperatures for various stages of development and species of fish are shown in Table 3.

The relation between increases in diurnal variations and growth rate is unknown. For some species, increases in diurnal variation might be beneficial. Biette and Green (1980) have demonstrated for sockeye salmon that temperature fluctuations, resulting from diurnal migrations throughout the thermoclines of stratified lakes, are associated with growth increases at low, and therefore realistic, ration levels. In contrast, Edwards et al. (1979) have shown for brown trout that increases in diurnal temperature fluctuations with constant mean temperatures result in diminution in growth. As noted earlier, streams often contain pockets of water cooler than the ambient stream (Keller and Hofstra 1982, Bilby 1984). These areas have been seen to be used by salmonids during times of stressful temperatures (Gibson 1966, Kaya et al. 1977), and may in part be responsible for the presence of salmon and trout in streams that occasionally attain very high temperatures (Bisson et al. 1985). However, the potential for this mechanism to assist in reducing thermal impacts to fish may be limited by the relative scarcity and, potentially, low oxygen concentration of cool-water areas (Bilby 1984).

Temperature is known to affect other physiological processes. For instance, as temperatures increase, diseases often become more virulent. The higher susceptibility to disease is brought on by a combination of higher metabolic rates and elevated levels of physiological stress. Ordal and Pacha (1963) and Parker and Krenkel (1969) report that a large number of common diseases of salmonids, including kidney disease, furunculosis, vibrosis, and columnaris, become more virulent as temperature increases. Nakatani (1969) found that columnaris became well established in salmonids at temperatures of 17 to 18°C under crowded conditions. When temperatures reached 21°C, the disease killed most of the infected individuals. Chinook and coho salmon and steelhead trout, infected with furunculosis, a bacterial infection, were held at temperatures ranging from 3.9 to 20.5°C (Groberg et al. 1978). At temperatures below 10°C, mortality of the fish ranged from 2 to 26% of

Table 3. Water temperature criteria, in degrees Celsius, for fish in western North America.

Species	Upstream Migration	Spawning	Incubation	Juvenile Rearing		
				Preferred	Optimum	Upper Lethal
Chinook	---	5.6-13.9	5.0-14.4	7.3-14.6	12.2	25.2
Fall	10.6-19.4	---	---	---	---	---
Spring	3.3-13.3	---	---	---	---	---
Summer	13.9-20.0	---	---	---	---	---
Chum	8.3-15.6	7.2-12.8	4.4-13.3	11.2-14.6	13.5	25.8
Coho	7.2-15.6	4.4- 9.4	4.4-13.3	11.8-14.6	---	25.8
Pink	7.2-15.6	7.2-12.8	4.4-13.3	5.6-14.6	10.1	25.8
Sockeye	7.2-15.6	10.6-12.2	4.4-13.3	11.2-14.6	15.0	24.6
Steelhead	---	3.9- 9.4	---	7.3-14.6	10.0	24.1
Kokanee	---	5.0-12.8	---	---	---	---
Rainbow	---	2.2-20.0	---	---	---	---
Cutthroat	---	6.1-17.2	---	9.5-12.9	---	23.0
Brown	---	7.2-12.8	---	3.9-21.3	---	24.1

Source: Adapted from Reiser and Bjornn 1979.

the infected fish. However, at 20.5°C, 93 to 100% of the infected fish died within two to three days. These investigations were conducted under conditions of constant temperature and high population densities. As with much of the temperature research, it is difficult to transfer work done in a controlled environment to a situation in the field. The virulence of various fish diseases under conditions of varying temperatures and relatively low population densities has seldom been examined.

An exception to the general rule of increased disease virulence with increased temperature was noted by Bisson and Davis (1976). They found a reduced infection rate of juvenile chinook salmon by the trematode parasite (Nanophyetus salmicola) for fish held in water 4°C warmer than a control. This seems to represent an instance where the infecting organism is less tolerant of temperature elevation than the host.

It is generally accepted that the temperature regime is one habitat component to which fish populations are locally adapted (Ricker 1972). For instance, Leggett and Carscadden (1978) demonstrated for the anadromous American shad (Alosa sapidissima) that the principal factor determining interpopulation differences in reproduction strategies was the variability in thermal regimes of the natal streams. Since developmental and metabolic rates in fish are highly dependent on temperature, variations in temperature lead to variation in the timing of such life history events as emergence and migrations. In lakes of the Fraser River drainage, interannual variations in sockeye salmon smolt sizes that are not accounted for by density appear determined by the length of the growing season, which, in turn, is determined by temperatures around the time of emergence (Goodlad et al. 1974).

Temperature variations around the time of smolt migration have been shown to be the principal source of interannual variability of Atlantic smolt migration timing in Norway (Jonsson and Ruud-Hansen 1985). Thedinga and Koski (1984) have shown, in their studies of the coho salmon of Porcupine Creek, Alaska, that variations in the timing of smolt outmigrations can have deleterious impacts on marine survival.

Since the timing of life history events is an adaptation to local conditions, it can be expected that changes in those environmental conditions, such as changes in temperature regimes caused by logging, may reduce the fitness of affected populations, with deleterious consequences to production (Leggett and Carscadden 1978). The possible effects of altering events such as fry emergence and smolt and adult migration have been mentioned in the context of logging effects (Narver 1972, Moring 1975b, Holtby and Newcombe 1982, Hartman et al. 1984), but with the exception of research at Carnation Creek, B.C., there has been little systematic study.

In a recently completed study, Holtby (1986) attempted to assess the effects of temperature on the timing of life history events of a population of coho salmon in a small coastal stream (Carnation Creek). Temperature-related impacts on this fish population were seen to bring about a series of changes: (1) logging-related (58%) and climate-related (42%) increases in late winter temperatures accelerated fry emergence (Holtby and Newcombe 1982, Tschaplinski and Hartman 1983); (2) increased length of growing season, resulting from earlier emergence, led to increased fry size entering their first winter (Hartman et al. 1984); (3) increased fry size led to higher overwinter survival (Holtby and Hartman 1982); (4) higher overwinter survival and size led to increased numbers and sizes of 1+ smolts; and (5) seaward migration of the smolts in spring was accelerated by seven to ten days.

The impacts of temperature increase on the freshwater phases of the coho population generally suggest increased production of smolts. However, earlier release to the sea of hatchery-stock coho smolts has been linked to decreased marine survival (Bilton et al. 1982). Therefore, the benefits that resulted from changes in smolt size and numbers following logging (Figure 11) may be substantially or wholly offset by increased saltwater mortality attributable to earlier migration.
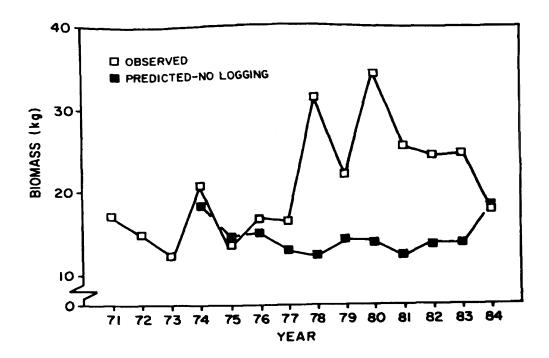
Figure 11.   The combined weight of coho salmon smolts produced by Carnation Creek, B.C. Logging began in the winter of 1975-76 and was largely complete in those areas of the watershed immediately surrounding anadromous salmon habitat by the summer of 1979. The line of predicted smolt output assumes that temperature changes associated with logging did not occur (Holtby 1986).

Several important points emerge from the studies at Carnation Creek, B.C. First, the alteration in the timing of life history events due to temperature changes may significantly affect fish production. Second, temperature effects are not necessarily confined to the stream, but ultimately may affect returns of adults to the stream. Third, the temperature changes that resulted in effects on fish production were relatively small and clearly not life threatening changes that occurred in the winter and spring. The much larger thermal effects of logging that were observed during the summer had no detectable effects on coho smolt production.

SUMMARY AND CONCLUSIONS

Stream temperatures in forested watersheds in the Pacific Northwest can be characterized as (1) predictable along such various spatial scales as latitude, elevation, and stream order, (2) predictable on temporal scales such as season and day, and (3) of low variability both between years and within days. It has been repeatedly demonstrated that removal of riparian vegetation alters stream temperature regimes. In coastal streams, where prolonged periods of below zero temperatures are rare, removal of riparian vegetation invariably results in increased mean and maximum stream temperatures and increased diurnal ranges. Over a sufficiently long period, effects of streamside

logging on thermal regimes can be detected throughout the year, and not just in the summer as is the general perception. In regions where winter temperatures are below freezing, the removal of riparian vegetation may result in the depression of stream temperatures and greater periods of freeze-up, but such situations have been little studied.

For a given stream, the magnitude of the temperature increase after streamside logging is proportional to the increase in exposure of the stream to incoming solar radiation, or, conversely, to the amount of shade reduction. Thus buffer strips (composed of vegetation not susceptible to blow down) are an effective means of providing shade and preventing temperature changes. The exact configuration and width of such buffer strips can be highly variable and site specific. In western Oregon, it appears that buffer strips 30 m or more in width along small streams provide approximately the same level of shading as an old-growth forest. More important, an understanding of the energy transfer influencing stream temperature permits the dimensions of streamside logging to be controlled to produce the desired effects on stream temperatures, ranging upward from no effects at all.

There are many reasons why the observed logging-related temperature increases have not had significant deleterious effects on resident salmonids. Among these are (1) the wide thermal tolerances of the freshwater forms of most of the resident salmonid species, (2) the natural diurnal cycling of stream temperatures, which limits exposure to maximum temperatures, (3) the occurrence of localized cool-water sources, which fish seem readily able to locate and utilize, (4) the inability to extrapolate tolerance limits determined under homogeneous laboratory conditions to the spatially and temporally complex thermal environments of streams, and (5) the ability of fish to migrate to other locations or to curtail activities temporarily when temperatures become stressful. Although increased summer temperatures remain a concern to fisheries managers, it appears that fish are generally able to tolerate such increases without major adverse impacts on growth or mortality.

Because of the extensive geographical range of salmonids, the effects of temperature on these fish should be viewed in a regional context. In at least some regions of the Pacific Northwest, concern over the lethal effects of elevated summer temperatures in small streams draining deforested watersheds is unwarranted. This is certainly the case in the low elevation, coastal streams of British Columbia and Washington. However, in other regions of the Pacific Northwest, increased temperatures from logging may remain a significant concern. For example, in southern areas (southern Oregon and northern California) and areas east of the Cascade Mountains, increased temperatures due to logging may have a greater impact on fish populations than in areas of cooler climate, because of ambient water temperatures. Unfortunately, for most of these areas little information is available that might demonstrate the influences increased water temperatures have on fish populations.

Temperature is clearly an important component of the habitat of many stream organisms, including the fish, and most organisms respond

to the changes in stream temperatures caused by streamside logging. But because temperature is only one of several closely interconnected physical factors that are affected simultaneously by streamside logging, it is questionable whether our understanding of the impacts of logging on fish production can be increased by trying to study the effects of temperature in isolation.

Increased temperatures following logging, together with increased light levels and increased nutrient concentrations, often lead to general increases in productivity in the trophic levels that form the basis of fish production. Increased temperatures, light, and nutrients all play a role. Temperature directly affects development rates of fish; in some systems, the temperature increases lead to earlier emergence, longer growing seasons, and increased survivals at critical times in the life histories of fish. Increased temperatures also directly affect metabolism and activity levels of fish.

The apparent generality of enhanced fish production after stream-side logging could be an artifact of geographically limited data or a "coastal rain-forest" perspective. For instance, there is relatively little known about the effects of logging on stream temperatures and fish production in areas where streams freeze in the winter. In such regions, production "bottlenecks" might occur during the winter period of low flows and freezing temperatures. Slight changes in stream exposure might cause decreased stream temperatures, and, coupled with other physical effects of logging such as channelization and decreased pool depths, could conceivably decrease winter habitat for fish and decrease production (Bustard 1985). Under such circumstances, enhanced summer production would be essentially nullified by worsened winter conditions.

The same streamside activities that lead to changes in *temperature* and light levels precipitate other changes in the stream (Bisson et al., Everest et al., Swanson et al., and Sullivan et al., in this volume). Streamside logging has often been associated with changes in sedimentation, bank stability, channel morphology, large woody debris, and other factors that ultimately alter the productive capacity of a stream for fish. Where sources of large organic debris have been removed, the effects of streamside logging on the physical configuration of the stream can extend for decades.

There are many promising areas for research on the impacts of streamside management on fisheries. There is a great need to develop empirical predictors of the productivity gains to be had from controlled streamside disturbance (In what situations should the streamside be left unaltered? If there are productivity gains to be had, how can streamsides be managed to maximize those benefits?). A great deal has yet to be learned about the processes governing the productivity of salmonids in the diverse stream types and climatic zones in the region. This knowledge is essential if the riparian zone is to be successfully managed. A technological challenge lies in the development of techniques that maximize the beneficial effects while minimizing or mitigating deleterious impacts.

Considering the productivity gains that may be had by judicious streamside treatments, it seems to us an overly conservative view to eliminate all forest management activity in the riparian zone. However, much remains to be discovered before managers can abandon their cautious stance on streamside logging. Therein lie the challenges for joint fisheries-forestry research.

ACKNOWLEDGMENTS

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