

HOW TIGHT IS THE LINKAGE BETWEEN TREES AND TROUT?¹

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Abstract: This paper explores the tightness of the linkage between stream-dwelling salmonids and riparian vegetation. Comparison of original distributions of salmonid species with that of vegetation types shows that distribution within a given salmonid species is not limited to a specific vegetation type, and that different salmonid species co-occur within a given vegetation type. Examination of reported differences in trout production among streams appear to be related to differences in riparian setting only indirectly and insofar as these reflect differences in prey availability and, to a lesser extent, differences in habitat features. Variability in trout production estimates are minimized when comparisons are species-specific and normalized for temperature differences among streams. Within a riparian vegetation type, the relationship between trout production and successional age of the streamside vegetation is often inverse.

Much of the research of the past decade on the land-water interface was triggered by Hynes' (1963) proposal that stream biota highly depends on the terrestrial setting and by Ross's (1963) observation that the distribution of many genera and species groups of stream invertebrates is closely correlated to the distribution of terrestrial vegetation types. All 14 (now 18) species of the genus *Pychnopsyche* (Limnephilidae), for example, occur entirely within the deciduous forest formation of eastern North America. Their distribution overlaps nearly perfectly with that of sugar maple (*Acer saccharum*), one of the dominant trees in the climax forest. Ross suggested that the coincident distributions occur because of the unique conditions imposed upon stream fauna by the nature of the forest itself.

This paper describes a study to determine if a linkage exists between stream-dwelling salmonid fishes and the surrounding terrestrial vegetation, explores native distributions of salmonid species with reference to the distribution of vegetation types, and evaluates the relationship between the riparian setting and trout population parameters.

Native Distributions of Salmonids in Relation to Vegetation

The native range of the salmonid family is the Holarctic realm, including northern latitudes of North America and Eurasia. Restricting consideration to the subfamily salmoninae, common genera include the chars, *Salvelinus* spp., the trouts, *Salmo* species, and the largely anadromous Pacific salmon, *Oncorhynchus*. In no case is the distribution of any of these genera delimited by the distribution of a specific vegetation type.

The distribution of individual species also is not generally delimited by the distribution of vegetation types. For example, the original distribution of brook char (*Salvelinus fontinalis*) was eastern North America from the Hudson Bay drainage and Labrador south to the southern Appalachian Mountains and west to parts of the Great Lakes basin and headwaters of the Mississippi drainage (MacCrimmon and Campbell 1969). This distribution coincides exactly with the hemlock and northern hardwoods region (Braun 1950), but it also encompasses other regions within the deciduous forest and boreal and tundra formations. The distributions of single species often extend beyond the range of a vegetation type among the trouts of western North America. Cutthroat trout (*Salmo clarki*), which were the most widely distributed of any western trout, occurred on both sides of the Continental Divide in the uppermost headwaters of the Columbia and Missouri river basins and in the Colorado River, Rio Grande, and Great Basin systems (Behnke 1972), across a range of vegetation types that included Pacific conifer forest, the Rocky Mountain forest complex, the Sierra Nevada forest complex, and the northern desert formation. In most geographical areas, the cutthroat trout do not form discretely differentiated populations, and variability among disjunct populations within a single drainage may be as great as the variability among drainage basins (Behnke 1972). Thus it is difficult to argue that any specific vegetation type posed a set of unique conditions that acted to limit the distribution of this salmonid.

Some *Salmo* species, notably within the golden trout complex (e.g. *Salmo aguabonita*, *S. gilae*, *S. apache*) do have very restricted distributions. *Salmo aguabonita* occurred originally in the Kern basin in California (Schreck and Behnke 1971), *Salmo apache* in the upper

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Salt River and headwaters of Little Colorado River, Arizona, and *Salmo gila* probably only in high gradient headwater streams of the Gila River in New Mexico (Lee and others 1980). Probably the vegetation surrounding the streams within these restricted ranges was originally fairly uniform in composition. Given the very broad geographic distribution of most freshwater salmonid species across a range of vegetation types, however, there is little reason to think that the relationship between the distribution of these trouts and the corresponding vegetation is causal in nature.

Present Distribution and Production of Salmonids in Relation to Vegetation

Salmonids, particularly the rainbow trout (*Salmo gairdneri*), brown trout (*Salmo trutta*), and brook char, have been extensively introduced to stream and river systems throughout the world (MacCrimmon 1971, MacCrimmon and Campbell 1969, MacCrimmon and Marshall 1968). The native range of the rainbow trout in western North America has been extended via introduction to every continent except Antarctica. The brown trout, native to Europe and Eurasia, has become established in all but 10 states in the U.S. and in 9 of 10 Canadian provinces.

In contrast to most stream invertebrates, salmonids and freshwater fishes in general are much more plastic in their responses to environmental conditions (Hynes 1970). Salmonids are obviously able to become established in streams that are surrounded by a broad array of vegetation types. An inescapable conclusion is that the composition of the surrounding vegetation of itself has not limited the ability of a salmonid population to inhabit a stream or river system.

Are any relationships apparent between composition of the streamside vegetative setting and trout population parameters other than distribution? These are not obvious. Similar production values have been reported among stream sites that differ in the nature of their vegetative setting. For example, the production of brook trout in Lawrence Creek, Wisconsin, a primarily open cropland stream bordered by some shrubs, was reported to be 18.1 (McFadden 1961) or 11.7 (Hunt 1974) g m⁻² yr⁻¹. In Valley Creek, Minnesota, which flows through northern hardwood forest, the annual production of brook trout was measured at 16.3 - 19.1 g m⁻², dropping to 7.9 g m⁻² in a year in which the stream experienced heavy siltation (Waters 1982). Similarly, the annual production of wild brown trout in a British Lake District stream, Black Brows Beck, which flows through oak dominated woodland, is within the same

range (10 g m⁻², LeCren 1969) as that of brown trout in a Danish stream (11.3 g m⁻² for 2 yrs, Mortensen 1985), Bisballe Baek, which is open with scattered alder and willow along its banks. Among sites with the same riparian setting, differences can be found in production (e.g., O'Conner and Power 1976). Considerable spatial and temporal variability in production can occur within the same stream system, confounding attempts to assess factors contributing to differential production among streams. Temporal variation can be extreme in populations of anadromous salmonids (Hall and Knight 1981).

Productivity incorporates two distinct components: 1) a weight component determined primarily by growth, and 2) a numerical component which represents the balance between births vs. deaths and immigration vs. emigration (Allen 1969). These two components and the factors regulating them may interact, but each is also affected by independent influences. Growth rate is dependent on both environmental and on genetic factors (LeCren 1965). The maximum size a fish will reach is determined by food availability, which may be density related. The rate at which maximum size is approached is under at least some genetic/physiological control. Brown trout are thought to show a higher temperature-specific growth rate than brook trout (which may explain why they tend to displace brook trout so readily in the eastern U.S.) - and thus productivity can be only fairly compared within species.

Growth rate of salmonids is also influenced to a very large degree by temperature (Elliott 1976). Assuming prey are available for consumption, higher growth is obtained at higher temperatures up to the optimal growth temperature; above this temperature, growth will again decline. Differences in trout production are minimized once one normalizes for temperature. For example, in a comparison of streams ranging from chalk streams in southern lowland Britain to brown water, upland streams in Scotland, Edwards and others (1979) found that the high growth rates of brown trout in chalk streams could be explained almost entirely on the basis of ambient temperature and in particular by the homeothermous nature of the temperature regime. In the Horokiwi stream in New Zealand, from which the highest trout production values have been reported (55 g m⁻² yr⁻¹, [Allen 1951]), the mean of monthly temperatures was about 2°C higher than any of the British streams described by Edwards and others (1979). This temperature increase may have contributed to the higher production values. Allen (1985) found that brown trout from the Horokiwi stream grew more rapidly than similar sized brown trout from Britain that were held at the same temperature and fed to satiation. He suggested that there may have been genetic selection for more rapid growth and a higher temperature limit.

Factors affecting the density component of productivity are not as straightforward. A fair amount of evidence suggests that for the adult segment of the population, the physical configuration of the stream channel limits the number of fish that can be supported (e.g. Hunt 1971, White 1975). The assumption, although often untested, that trout standing crop can be predicted from habitat variables such as pool area or volume, bank cover, etc. has formed the basis of a burgeoning development of habitat models. Except under conditions of heavy fishing pressure, the density of adult freshwater fish populations is often fairly stable, which can be partly attributed to the long life span of reproductive stages. This may not hold for juvenile stages, which are extremely variable, and the principal cause of variation in overall population abundance. Much of the growth and up to 98 percent of the mortality takes place in the post-hatching, pre-maturity part of life (LeCren 1965). The factors responsible for this are the least understood and most problematic aspects of fish population dynamics. It is not at all clear, for example, whether any increase in the density of fry will be translated into an increase in the density and/or biomass of the adult population. Certainly future research on forestry-fishery interactions need to focus on this stage.

Functional Links Between Riparian Vegetation and Salmonid Populations

The above considerations aside, it is reasonable to conclude that food availability, temperature, and physical aspects of the channel are three of the major determinants of productivity. These determinants are strongly affected by the nature of and functional roles played by riparian vegetation, even though trout distribution patterns and productivity cannot be tied in a direct fashion to the composition of the streamside vegetation.

Temperature Effects Associated with Riparian Vegetation

In terms of its effect on stream temperature, the most important distinction to make among types of riparian vegetation is whether the vegetation provides an open or a closed canopy. In headwater streams this distinction will separate grasses and herbaceous vegetation from some deciduous and coniferous trees, depending upon stream width. In very small streams, even grasses may effectively shade the channel, especially if sideslopes are steep and banks undercut. In summertime, the principal source of heat to a small stream comes from direct solar radiation (Beschta and others 1987); canopy closure may reduce incoming radiation by 85 percent (Brown

1983). Canopy closure may also prevent heat loss in the winter that can occur by evaporation, convection, and long-wave radiation. Trout have been observed to feed actively during the winter, but the energy gain from feeding is often sufficient only for maintenance and not growth. An increase in winter temperatures, however, may promote greater growth. Increases in summer maximum temperatures following canopy removal generally range from about 3 to 10°C in the U.S. (Beschta and others 1987). In mountainous streams the increase in maximum summer temperatures does not usually approach the tolerance limits for resident salmonids; this is often a very significant problem in low gradient, low elevation sites. Even in mountainous streams, however, increases in the temperature regime may shift fish community composition to favor species other than salmonids (Karr and Schlosser 1978). For example, Reeves and others (1987) found that temperature affected the outcome of competitive interactions between steelhead trout and reddsideshiner (*Richardsonius balteatus*). Trout production at cool temperatures was the same in the presence and absence of the shiner; at warmer temperatures (19-22°C), trout production decreased 54 percent in the presence of the shiner.

Influence of Riparian Setting on Food Availability to Trout

The open or closed nature of the canopy also has an important effect on food availability to trout, for at least two reasons. First, light intensity appears to affect the foraging efficiency of trout. Wilzbach et al. (1986) found a strong log-linear relationship between trout foraging efficiency and surface light in an Oregon Cascade Mountain stream. Second, degree of canopy opening plays a major role in determining the food resource base for the invertebrate prey community and its consequent composition. The resource base of small woodland streams is heterotrophic, i.e. dependent upon organic matter elaborated in the surrounding terrestrial system (e.g. Cummins 1974, Cummins and others 1984). In these streams, shredders which feed on coarse particulate organic matter derived from the terrestrial zone comprise a large and often dominant component of the invertebrate community (e.g. Cummins and others 1981, Petersen and others 1988). In larger stream or river systems and in small streams lacking a canopy, in-stream algal production increases and scrapers which use this food resource may largely replace the shredder component. A distinction between scrapers and shredders is an important one because shredders rarely comprise a significant part of trout diets. As a general rule, salmonids feed upon invertebrates as they drift in the water column. Shredders are not often found in the drift, except at times of emergence or in very early life stages, at a size below which salmonids typically detect prey items. Many

scrapers, especially heptageniid and some ephemereiid mayflies, are more commonly collected in drift samples. The most common prey items in trout diets, however, belong to the functional feeding group of collectors, including baetid mayflies, many chironomid midges, and blackflies which feed on fine particulates derived from litter or algal detritus by filtering or gathering. These exhibit an even greater propensity to drift, often on a predictable diurnal schedule.

In relation to its effect on food availability, the other important distinction to make among different types of riparian vegetation is the turnover time of its litter inputs to the stream. These can be roughly broken down into fast or slow. The fast litter category includes many herbaceous plants, shrubs characteristic of recovery stages from a disturbance (such as alder, dogwoods, viburnums, and salmonberry), as well as some types of deciduous trees such as basswood, elm, and black cherry. The slow litter category includes grasses and sedges, shrubs such as the rhododendrons, conifers, and such deciduous trees as oaks and beeches. If litter is derived predominantly from 'fast' plants, there will be a rapid turnover of coarse particulate organic matter (CPOM) relative to the time of input and a rapid generation of fine particulates (FPOM), including a significant portion derived from shredder feces. If litter comes from 'slow' plants, there will be a delayed turnover and generation of CPOM and FPOM. Quickly decomposing litter supports a fall-winter population of shredders and collectors feeding on this allochthonous detritus. Slowly decomposing litter supports delayed spring-summer populations of shredders and collectors.

The combination of turnover time of the litter and the open or closed nature of the canopy may predict the availability and productivity of the food base for salmonids. Food availability can be considered as the sum of density of prey multiplied by prey turnover and the fraction of the community that regularly drifts (i.e. collectors and some scrapers). An open canopy stream should produce a greater availability of food for trout than would closed canopy streams, irrespective of the turnover time of the litter inputs, because of the year-round sustained yield of scrapers and availability of high quality algal-derived detritus as the food base for collectors. Predominantly fast litter inputs should provide greater food availability than slow litter inputs because they would favor collector development in the autumn and winter during times of lower algal production which in turn would support lower scraper populations and provide less algal detritus. Thus in general, the expectation should be that food availability increases in streams from closed canopy, slow litter/closed canopy, fast litter/open canopy, slow litter/open canopy, fast litter.

Streams with an open canopy and fast litter are characteristic of early stages in a successional sequence. The

succession will lead over time to a closed canopy with fast litter if mature vegetation is deciduous, and providing that the climax vegetation is not oak, sycamore, or beech; or to a closed canopy with slow litter where the mature vegetation is evergreen, oak, sycamore, or beech. Differences in food availability are the most likely explanation for the inverse relationship that has often been observed between trout production and successional age of the streamside vegetation (Murphy and others 1981, Murphy and Hall 1981, Hawkins and others 1983, Bisson and Sedell 1984, Wilzbach 1984).

Riparian Influence on Channel Configuration and on Cover

The riparian setting influences channel configuration through its effect on bank stability, and through the provision of woody debris into the stream channel, which affects local hydraulic conditions and sediment deposition (Sullivan and others 1987). Both overhanging vegetation and its root systems, and in-channel debris may provide cover for salmonids. Bank stability is enhanced by dense root systems, and distinctions can be made among riparian vegetation according to root mass density. Deciduous trees have deeper root systems than coniferous trees. Herbaceous plants and shrubs, particularly those characteristic of pioneer stages, develop large, dense root systems very quickly. These often act to constrict channel width by preventing erosion; this forms the basis of White and Brynildson's (1967) suggestions for improvement of trout habitat by replacing streamside trees with shrubs. However, during extremely highwater discharges, long term bank stability and location may be better served by tree root systems than by shrubs. In Sequoia National Park, streams can be observed flowing between giant sequoia trees that are in the range of 1000 yrs. old.

The role of woody debris in influencing channel configuration and the biological properties associated with woody debris have been recently reviewed by Sullivan and others (1987) and Bisson and others (1987). Briefly, in-channel debris acts to form pools and to control sediment and organic matter storage. Its importance to salmonids lies primarily in pool formation and backwater areas for rearing, and in the provision of cover from high flow or from predators. Distinctions to make among riparian vegetation with respect to these functions include the amount and size of debris that is available for input to the channel, and the decomposition time of the wood in the channel. Coniferous trees are able to supply larger amounts of wood than most deciduous trees and, in general, have slower decomposition rates.

There is an interesting thing to note about cover. A ranking of cover by the amount supplied and its duration within the stream channel proceeds in the opposite

direction from a ranking of food availability as described earlier. Cover should be greatest in streams with closed canopies and slow litter, and should decrease in order of closed canopy, fast litter/open canopy, slow litter/to open canopy, fast litter. This is a further indication that salmonid production generally tracks food availability rather than cover, and suggests either that food availability is of greater importance to salmonid production than cover, or that we haven't fully deciphered the interaction between food and space. Laboratory experiments on the relative roles of food abundance and cover in determining the distribution and emigration of cutthroat trout support the suggestion that food overrides cover in importance (Wilzbach 1985).

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