

Influence of Forest Practices on Aquatic Production

S. V. GREGORY, G. A. LAMBERTI, D. C. ERMAN,
K. V. KOSKI, M. L. MURPHY, and J. R. SEDELL

ABSTRACT Management of streambanks for fishery resources requires a thorough knowledge of the structure and major processes of stream ecosystems. Management of streamside forests must be based on a functional perspective of riparian zones that integrates geomorphic processes, terrestrial plant succession, and aquatic ecology. Forestry practices potentially alter solar radiation, water temperature, sediment, nutrient, and litter inputs, woody debris, and channel structure--all of which influence the habitat and nutritional resources of aquatic organisms. Primary producers are generally stimulated by canopy removal and the increases in nutrients and temperature that often accompany timber harvest, but instability of stream sediments may decrease plant abundance. Microbial processes may be enhanced by increases in nutrients, detrital quality, and temperature, but microorganisms may be negatively affected by a decreased quantity of detritus or decreased oxygen concentrations. The ability of streams to retain algae and litter inputs for food resources and retain sediments for habitat is determined by channel complexity, especially accumulations of woody debris. Aquatic insects and other invertebrates respond to changes in habitat and food resources. Sedimentation and decreased substrate stability may decrease the abundance of aquatic insects. Herbivores benefit from stimulation of aquatic plants; detritivores may be negatively affected by the changes in detritus. Frequently, insect community structure shifts toward organisms that are more likely to drift, thereby increasing the availability of food for salmonids. Salmonids also more efficiently capture prey items in open areas where light intensities are greater. These potential benefits may be negated if thermal tolerances are exceeded by temperature increases, if sediments blanket rearing and spawning habitat, or if winter habitat is reduced. Changes in habitat, food, or temperature may also alter fish community structure and potentially increase competition with the species of interest.

Streams in harvested watersheds may therefore be more productive, but the abundance and distribution of organisms in these streams may fluctuate more than in streams in mature forests. Resource objectives must be clearly defined before fishery resources can be effectively managed in forest ecosystems. The landscapes and biotic communities of terrestrial and aquatic ecosystems are intricately linked, and effective management must acknowledge and incorporate such complexity.

STREAM ECOSYSTEMS

Management of streams and adjacent riparian zones resources requires a thorough knowledge of the structure and processes of stream ecosystems. Management efforts frequently focus on a limited set of habitat or food requirements of fish, such as instream flows, pool volumes, temperature, spawning substrate, sedimentation, and cover. Such approaches may accurately address particular issues related to land use practices, but they are inherently limited because they ignore major attributes of stream ecosystems that are required to support the fisheries of interest.

The food base in streams comprises autochthonous matter (aquatic primary production) and allochthonous organic matter (leaves, needles, wood, soil, grass). Microbial communities in streams use particulate detritus and dissolved organic matter as their energy source. The supply of plants, detritus, and associated microorganisms determines the abundance and community structure of consumers. Invertebrate consumers in streams include herbivores, which consume living plants, detritivores, which feed on dead organic matter, and predators, which consume other animals. These organisms serve as food for vertebrate predators, such as salmon, trout, sculpin, and salamanders.

Riparian zones have been investigated and managed from many points of view. Often particular plant community associations or soil moisture conditions are used to delineate riparian boundaries. This perspective was developed by plant ecologists for studying plant communities in wet habitats, but it offers little to resource scientists who are concerned with critical physical and biological processes that influence fisheries and wildlife in and along streams, rivers, and lakes. Functional perspectives of riparian zones developed by Meade et al. (1977) and Swanson et al. (1982) define riparian zones as two-dimensional zones of direct interaction with aquatic ecosystems, extending outward from the channel to the limits of flooding and upward into the canopy of streamside vegetation (Figure 1). This perspective can be applied to any ecosystem process, but critical functions for stream ecosystems include shading, inputs of litter and coarse woody debris, uptake of nutrients, bank stabilization, and interaction of sediments.

This simple functional model identifies the primary influences of riparian vegetation on aquatic ecosystems, but does not address the events and processes that initially create development of riparian plant communities. Riparian zones are located in a portion of the watershed that frequently experiences flooding and therefore are spatially and structurally complex. Concepts of riparian zones must include physical and biological processes that create riparian settings. Geomorphic processes and features create and modify the structure of stream channels and floodplains. The resulting mosaic of geomorphic surfaces determines the spatial pattern and successional development of riparian vegetation, and this physical setting and associated vegetation provide the template that determines the structure and function of stream

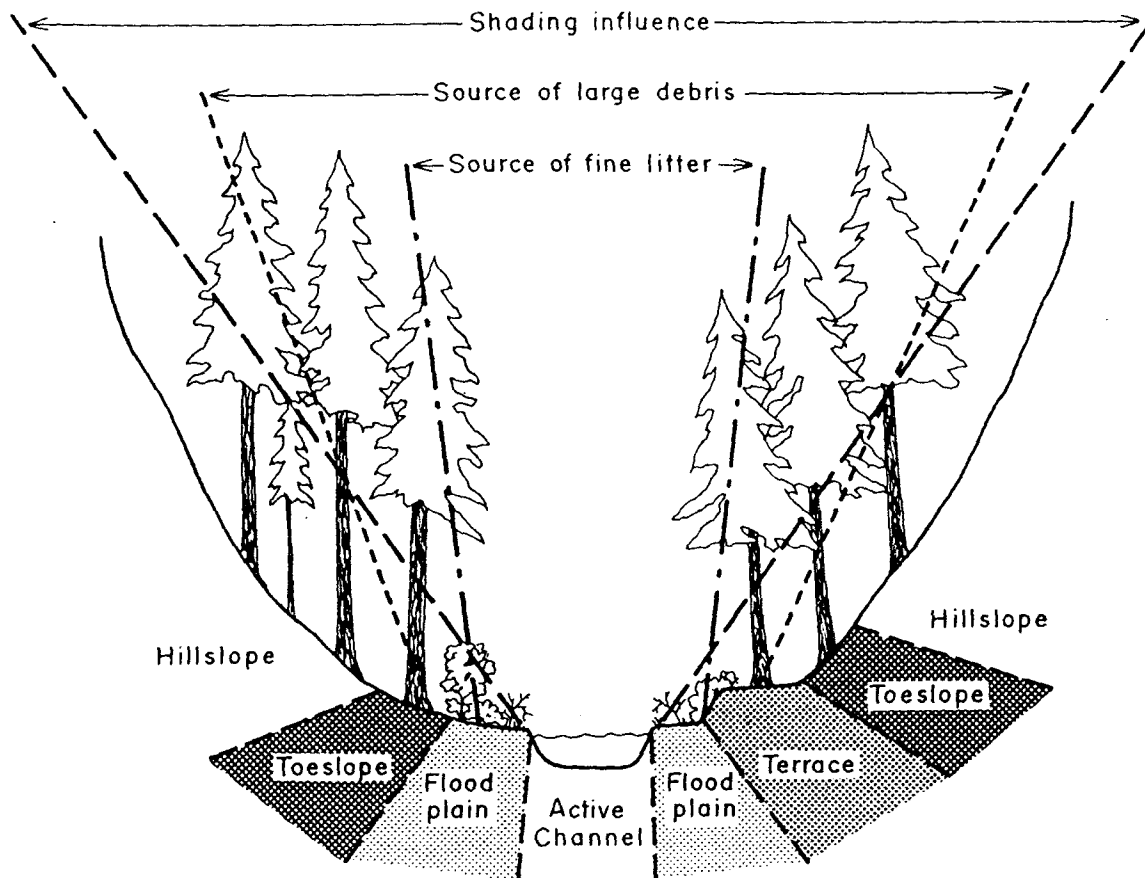


Figure 1. Diagrammatic representation of a functional perspective of riparian zones (from Meehan et al. 1977).

ecosystems. This perspective of riparian zones not only identifies major linkages between terrestrial and aquatic ecosystems but also incorporates physical processes that create and modify landforms along river valleys.

ALTERATION OF STREAM ECOSYSTEMS BY FOREST PRACTICES

Forestry practices potentially alter the structure and composition of the riparian zone and thereby influence the environment and structure of streams and rivers. Canopy removal allows more solar radiation to reach the water surface. A portion of this radiation is absorbed by the water itself and converted to heat energy, increasing the temperature of the stream. Another portion of this light energy is used by aquatic plants (algae, mosses, and macrophytes) to drive the photosynthetic mechanism and potentially increase rates of primary production.

Removal of the vegetation also removes the source of leaves and wood for streams. The amounts of leaves, needles, and twigs that

annually rain down from the canopy are reduced, and the composition of this matter is shifted for fifty to eighty years. The source of coarse woody debris to stream channels is lost for more than a century, and the composition of woody inputs shifts from coniferous material, which is relatively decay resistant, to deciduous material, which is more rapidly decomposed.

Timber harvest and associated road building lead to increased rates of erosion into stream channels, and this alters substrate composition within the channels. Channel disruption, decreased rooting strength, removal of debris from channels, and elevated sediment loading decrease the stability of channel morphology and the stream substrates. These changes in the environment and structure of stream systems have profound implications for stream ecosystems.

Primary Producers

Riparian vegetation strongly influences primary production in lotic ecosystems through attenuation of light energy. This influence is most pronounced in small, headwater streams where there is little if any canopy opening and less than one percent of total solar radiation reaches the stream. As streams become larger in a drainage, the opening in the canopy over streams widens and the amount of solar radiation reaching the channel increases. As a result, production of aquatic plants increases correspondingly (Hall 1972, Sumner and Fisher 1979, Naiman and Sedell 1980, Gregory 1980, King 1983, Minshall et al. 1983). In large rivers, riparian vegetation exerts a minor influence on aquatic primary production. The effects of forest practices on aquatic primary production therefore will be most strongly exhibited in small, headwater streams.

Many studies have demonstrated that removal of riparian vegetation during timber harvest stimulates aquatic primary production (Dever 1962, Hansmann and Phinney 1973, Busch 1978, Gregory 1980, Murphy et al. 1981). This period of enhanced primary production will last until development of the second-growth canopy results in light intensities similar to those of mature forest conditions. Rates of primary production increase linearly with increasing light energy at low light intensities below a threshold of light saturation, but rates of primary production do not increase with increased light intensity above this threshold. Saturation of photosynthesis in benthic algal communities in streams occurs at approximately 20% of full sunlight. Therefore, it is important to recognize that more radiation will not necessarily increase primary production if light intensities are already sufficient to saturate photosynthesis. In headwater streams of the Cascade Mountains, we commonly observe that light intensities rarely exceed 5% of full sunlight in mature forests, range from 5 to 15% of full sunlight in second-growth forests, and range from 30 to 100% of full sunlight in recent clearcuts. Also, supply of nutrients will have little if any effect on aquatic primary production at low light intensities, because photosynthesis is limited first by light intensity; therefore, shading by streamside vegetation can override the potential stimulation of primary production by nutrient inputs (Gregory 1980).

Primary production in streams in the Pacific Northwest is potentially limited by nutrient availability, particularly at high light intensity. In general, surface waters in areas of volcanic geology exhibit relatively low concentrations of inorganic nitrogen, both nitrate and ammonium, and relatively high concentrations of inorganic phosphorus. These are the only forms of these nutrients that can be used by aquatic plants in primary production. In a survey of more than seventy-five streams in western Washington, Thut and Haydu (1971) found that primary production in streams draining volcanic landforms was more likely to be nitrogen limited, but primary production in streams in glacial or granitic geology was more likely to be phosphorus limited. Studies of primary production in basalt-dominated areas of the Cascades have demonstrated that increased concentrations of nitrate-nitrogen stimulate primary production (Speir 1979, Gregory 1980, Triska et al. 1983). Investigations throughout the United States have found that concentrations of nitrate are elevated for several years after logging (Fredriksen 1971, Likens et al. 1970). Generally, nitrate concentrations return to preharvest levels within the first decade as watersheds revegetate; therefore, stimulation of primary production by increased nutrient concentrations resulting from logging will generally be limited to the first decade after harvest.

Timber harvest frequently results in increased stream temperatures (Brown and Krygier 1970), and rates of gross primary production generally increase with increased temperature (Phinney and McIntire 1965). Although elevated temperature will increase rates of gross primary production, rates of respiration by benthic communities will generally increase at an even greater rate; therefore, net production of organic matter will be decreased. In laboratory studies, temperature increases of 10°C increased rates of gross primary production by only 30% and had no effect on primary production at light intensities greater than 10% of full sunlight. Responses to changes in light intensity as a result of canopy removal potentially are far greater than the increases in primary production that would result from an elevation in stream temperature of a few degrees.

Changes in light intensity, nutrient supply, and temperature after logging potentially increase rates of primary production, but increased production may not result in substantially greater standing crops of algae if aquatic herbivores respond to the greater food availability. Many studies have observed that standing crops of algae are greater in streams in clearcuts than in streams in mature forests (Hansmann and Phinney 1973, Stockner and Shortreed 1976, Gregory 1980, Murphy et al. 1981, Rounick and Gregory 1981). Increases in standing crops of benthic algae may not adequately reflect the increased primary production if this material is heavily grazed by aquatic invertebrates. Many laboratory investigations in the Pacific Northwest have demonstrated that grazers may decrease standing crops of benthic algae substantially (Speir 1979, Gregory 1980, Sumner and McIntire 1982). In California streams, grazing caddisflies reduced standing crops of algae to 10% of algal standing crops on ungrazed substrates (Lamberti and Resh 1983). Effects of land use practices on aquatic primary producers often are evaluated in terms of algal abundance, but it is important to remember that these primary producers are components of tightly linked

food webs. Increased primary production may be expressed as increased growth and survival of consumers, with little apparent change in algal abundance.

Allochthonous Organic Matter

Terrestrial vegetation along streams and rivers contributes leaves, needles, and wood to stream ecosystems. This material produced outside the aquatic ecosystem is termed allochthonous organic matter and represents the dominant source of organic matter in undisturbed, head-water streams (Fisher and Likens 1973, Triska et al. 1982, Cummins et al. 1982). Removal of the forest canopy by timber harvest greatly alters the quantity and quality of organic matter available to higher trophic levels in stream ecosystems. Annual litterfall decreases from approximately 300 to 400 g/m² per year in mature forests to less than 100 g/m². Decreased allochthonous inputs persist for ten to twenty years, but second-growth stands that are dominated by willow, alder, and maple may contribute more than 400 g/m² per year. The effect of logging on the quantity of coarse particulate organic matter (excluding wood) delivered to streams from the surrounding forest will generally be restricted to the first few decades after harvest. This initial period of reduced allochthonous resources will be extended at higher elevations.

The period during which logging affects the total amount of allochthonous organic inputs to streams is limited to a few decades, but the changes in quality of allochthonous organic matter will last for thirty to one hundred years, depending on stand characteristics. Second-growth stands along streams and rivers are dominated by deciduous trees and shrubs. The foliage of these plants generally has higher nitrogen content, lower lignin content, and lower concentrations of chemicals that inhibit microbial activity. As a result, the quality of deciduous litter as a nutritional resource for microbial communities and consumers is higher than that of coniferous litter. Rates of leaf decomposition are much faster for deciduous leaves than for coniferous needles (Triska et al. 1982); an alder leaf will completely decompose within six months after falling into a stream, but a Douglas-fir needle will require just less than a year for complete decomposition. These rates largely reflect the microbial decay of the litter, but aquatic invertebrates can have an important effect in the loss of coarse particulate organic matter (Petersen and Cummins 1974, Sedell et al. 1975). The microbial colonization and modification of the organic matters, a process known as conditioning, plays an important role in the consumption of detrital resources by aquatic invertebrates. Invertebrates will selectively consume conditioned leaves, and the rate of conditioning is closely linked to the rate of decomposition (Cummins 1974).

Most studies of allochthonous organic matter in stream ecosystems have focused on inputs from trees, but herbaceous plants and shrubs are major sources of allochthonous organic matter for streams. The opening of the canopy after logging increases the production of herbs and shrubs along streams. Although herbs and shrubs contribute lower quantities of organic matter, the quality of this allochthonous material is

generally even higher than that of deciduous litter. Recent studies in streams in the Cascade Mountains revealed that many herbs and shrubs, such as coltsfoot, devil's club, and fireweed, completely decompose in thirty to sixty days, a rate that is two to six times faster than decay rates for alder leaves. Herbs and shrubs tend to grow within the active stream channel and become available to consumers when they are inundated by rising flows in early fall storms. Much of this material requires little if any conditioning before being consumed by invertebrates, and therefore contributes quickly to higher trophic levels.

Most decomposition of detritus occurs aerobically in streams of the Pacific Northwest, but certain depositional areas may be sites of anaerobic microbial activity. Large quantities of organic and inorganic matter are stored in debris jams, toes of debris torrents, and beaver dams. Intragravel flow of water through these habitats can be a substantial portion of total discharge, and these areas can exert major influences on downstream reaches. The high rates of microbial activity in the stored organic material can create localized anaerobic conditions. Rates of decay are slower in these anaerobic zones, but important nutrients for aquatic organisms are produced by anaerobic microbial processes and the chemical environments in these habitats. Concentrations of ammonium and orthophosphate increased by an order of magnitude below beaver dams in streams in the Coast Range (C. N. Dahm and J. R. Sedell, pers. comm.). The influences of such features in streams are complex, but chemical transformations that are associated with these habitats can be important to downstream reaches.

Retention

Streams commonly are considered as nothing more than conduits that transport material from watersheds; but streams efficiently trap both organic and inorganic matters entering their channels from the surrounding landscape, a process that is extremely critical to aquatic organisms. Organic matter cannot serve as a nutritional resource for aquatic biota until it is retained within the stream channel. Similarly, inorganic substrates cannot serve as habitat until they are trapped and stored. The availability of food and habitat for aquatic organisms is linked closely to the retention characteristics of stream channels, which are strongly influenced by forestry practices.

Material in transport in a stream channel is retained by either passively dropping out of transport and settling to the stream bottom or being actively trapped against another object; therefore, retention is closely linked to the morphology of the stream channel and the composition of the streambed. During low flow conditions, pools function as depositional zones where particulate matter drops out of transport; and riffles are shallow, high velocity zones where material is trapped against substrates. At high flow, this pattern of velocities reverses. Pools become high velocity, erosional areas; riffles exhibit lower velocities than pools and are areas of deposition.

The retentive characteristics of stream channels are closely linked to the nature of adjacent riparian zones. As channel roughness

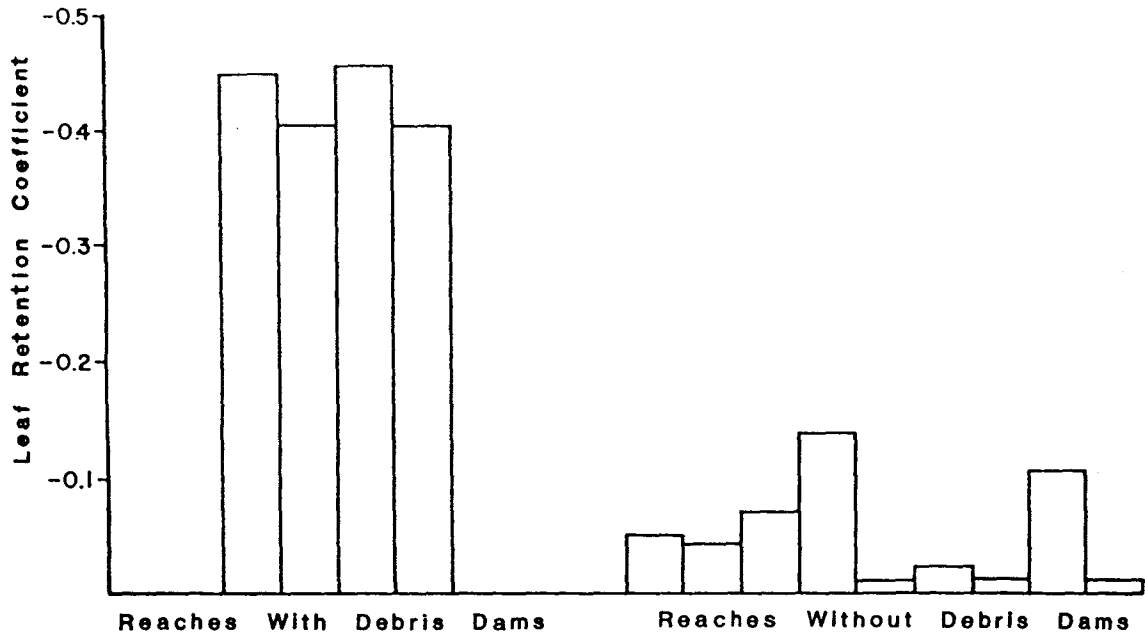


Figure 2. Rates of leaf retention in stream reaches with and without debris dams (from Speaker et al. 1984).

increases, the retention efficiency of a reach increases (Speaker et al. 1984). One of the major roughness elements in stream channels of the Pacific Northwest is woody debris. A comparison of leaf retention in streams of the west slope of the Cascade Mountains demonstrated that stream reaches with debris dams were more than four times as retentive as reaches without debris dams (Figure 2, Speaker et al. 1984). Effective retention requires not only large woody debris that creates stable retention sites but also smaller woody debris, such as branches, sticks, and twigs, that essentially creates a sieve through which the stream flows. In studies of retention in more than twenty streams in the Cascades and Coast Range, more leaves were trapped on small woody debris than on any other channel component (Speaker 1985, Speaker and Luchessa, unpublished manuscript). Timber harvest in riparian zones removes the sources of woody debris for the stream channel and reduces the loading of wood for many decades. Removal of large trees decreases the source of large wood that creates stable, persistent debris accumulations in channels. The complex array of different sizes and types of woody debris in streams greatly influences the ability of streams to retain organic matter, and reduction of this material by timber harvest affects the food resources and habitat for aquatic organisms.

Macroinvertebrates

Macroinvertebrates are essential components of food webs in streams, where they consume both autochthonous and allochthonous organic matter (Lamberti and Moore 1984). Most aquatic invertebrates function as primary consumers (feeding on primary producers and

decomposers) or detritivores (feeding on dead plant material). A smaller proportion of macroinvertebrates are predators, mostly feeding on other invertebrates. Stream invertebrates are important dietary items for vertebrate predators such as fish and salamanders. Thus changes in invertebrate community structure resulting from forestry practices can have significant effects on stream fishery resources. Responses of invertebrate communities to timber harvest are poorly understood, but several recent studies demonstrate that invertebrates are sensitive indicators of environmental change in harvested watersheds (Newbold et al. 1980, Murphy and Hall 1981, Murphy et al. 1981, Hawkins et al. 1982).

Lower gradient streams that have been clearcut (unprotected by buffer strips) and that accumulate significant amounts of fine sediment in the streambed may show reduced densities of benthic macroinvertebrates. This is attributable to several factors, including (1) reduction of available habitat for macroinvertebrates as interstitial spaces in the streambed substrate are filled by fine sediment, (2) elimination of hyporheic habitats (deep subsurface zones that serve as important habitat for certain taxa or specific age classes of macroinvertebrates) due to filling of interstitial spaces with fine sediments or reduction in dissolved oxygen concentration, (3) changes in food availability, such as reduction in food quality of fine particulate matter, and elimination or burying of periphyton communities, and (4) physical abrasion of substrates by fine sediments, resulting in direct mortality or increased drift of macroinvertebrates. Higher gradient streams that maintain a coarse substrate (i.e., display minimal sedimentation) may respond to increased incident sunlight following clearcutting with increased rates of primary production. Invertebrates that utilize periphyton as a food source or as habitat consequently may increase in abundance in these well-lighted streams. This increase in the density of primary consumers may also result in increases in the abundance of their invertebrate predators, such as setipalpiian stoneflies (Plecoptera) and rhyacophilid caddisflies (Trichoptera).

In most instances, shifts in the abundance and taxonomic composition of benthic invertebrates will occur in streams that drain logged watersheds. Disturbed stream habitats will favor vagile, opportunistic species that have high reproductive rates, including midge larvae (Chironomidae) and mayfly nymphs (Ephemeroptera), such as occurred in logged watersheds of northern California (Figure 3). Recolonization of defaunated stream habitats by macroinvertebrates will occur by three major mechanisms: (1) drift, which is the downstream transport of benthic animals by the water current, (2) aerial oviposition, which is egg laying by adults of aquatic insects, and (3) benthic movement, which is active locomotion on or through the sediments from upstream, downstream, or hyporheic habitats. Shifts to herbivore-dominated communities can occur as a result of increases in primary production. In conjunction with decreased loading of large particulate organic matter, there will be fewer species of invertebrates that process coarse detritus.

The increase in herbivorous macroinvertebrates with canopy opening in logged basins often results in an overall increase in

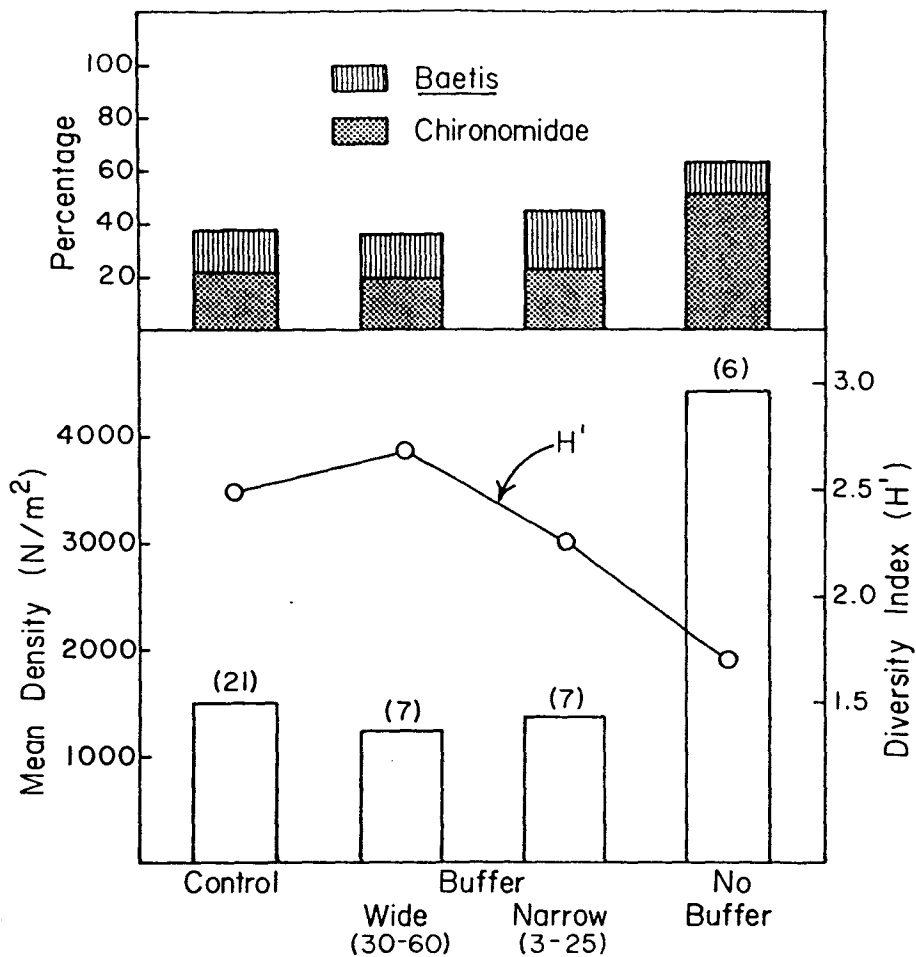


Figure 3: Mean densities and diversity indices of macroinvertebrate communities in streams with and without buffer strips in northern California (from Newbold et al. 1980). Percentages of *Baetis* and *Chironomidae* of total invertebrate populations are illustrated in upper histogram.

macroinvertebrate density for several years following timber harvest (Murphy et al. 1981). For example, in a comparison of several watersheds in northern California that had differential levels of stream protection, macroinvertebrate density increased by three times in the stream that had no buffer strip (Erman et al. 1977). Densities were comparable in buffer-stripped and control streams. Increased densities of macroinvertebrates in well-lighted streams, especially drifting forms such as mayflies, may result in increased abundances and production of visual predators, such as salmonids and salamanders (Murphy and Hall 1981).

The aerial adult stages of many species of aquatic insects rely on riparian vegetation in which to complete the reproductive phase of their life cycle. Egg maturation, mate location, and mating largely occur in or around riparian vegetation. In addition, riparian vegetation influences longevity, dispersal, colonization patterns, and oviposition site selection

of aquatic insects. Removal of riparian vegetation will interrupt this phase of the life cycle, in addition to exposing aquatic insects to unfavorable temperature and humidity conditions. In this case, recruitment of eggs to the stream may depend on the movement of adults from neighboring, intact watersheds. Because most adult aquatic insects are poor fliers and move only a short distance from where they emerge, colonization of streams in logged watersheds may rely on strong (rare) fliers or, more likely, on wind-borne transport of small insects. The taxonomic composition of the invertebrate community may reflect this differential recruitment of adults and eggs to the stream.

Estimates of species diversity that incorporate evenness and richness parameters (e.g., Shannon, Simpson indices) frequently decline in streams in logged watersheds, because systems become dominated by a few successful species (i.e., evenness declines), even though other species may be present in remnant numbers (Erman et al. 1977). Changes in species richness (number of species) may be less apparent, because decreases in taxa of some feeding guilds (e.g., detritus processors) may be compensated for by increases in other guilds (e.g., grazers and predators). Newbold et al. (1980) showed that Shannon diversity declined in streams within several northern California clearcuts that were not protected by buffer strips or that had very narrow buffer strips (Figure 3). However, Shannon diversity in streams that had 30 m buffer strips was indistinguishable from that in streams in unlogged watersheds.

Streams that are unprotected by buffer strips in logged watersheds may accrue large standing crops of benthic algae because of increased incident sunlight. Herbivores such as grazing mayflies (e.g., *Baetis*, *Heptagenia*, *Drunella*), midges (Chironomidae), and micro-caddisflies (Hyproptilidae) will respond to this food resource with increases in densities and secondary production. Coincident with the increase in herbivores is a decline in densities of detritivores due to reduced loading of large organic debris. The amount of woody debris in the stream may remain high for some time because of the presence of slash, thus favoring detritivores. However, following slash burning or over a longer period, loading of organic debris (e.g., wood and autumn-shed leaves) will decline, thus resulting in reductions in detritivore abundance. The increase in primary consumers within clearcuts may often overwhelm reductions in the detritivore component of the invertebrate community. For example, Newbold et al. (1980) reported increased densities of invertebrates in streams within clearcuts, in particular higher abundances of vagile primary consumers such as *Baetis*, *Nemoura*, and various Chironomidae that were associated with increases in rates of primary production. Predators (both invertebrate and vertebrate) may respond to this improved food resource with increased density, biomass, and species richness, as demonstrated for several Oregon Cascade Mountain streams (Murphy and Hall 1981).

Changes in the food resource base (e.g., increased periophyton, decreased allochthonous detritus) will produce concomitant changes in the proportions of functional feedings groups of invertebrates. Blooms of benthic algae will favor invertebrates that remove growth from

substrate surfaces (scrapers) or penetrate algal cells with specialized mouthparts (piercers). Reductions in the abundance of large particulate detritus will disfavor invertebrates that skeletonize or chew leaves (shredders) or burrow into wood (gougers). Dynamics in food resource abundance can be transferred to changes in secondary production, an index of consumer abundance that combines estimates of population survivorship and individual growth into a single measurement. The response in secondary production to timber harvest will vary spatially, temporally, and with specific taxa. After logging, increases in primary production will favor colonization by vagile herbivores that can complete several generations per year. Although total biomass may show little increase, a shift to such multivoltine species may result in increased secondary production. Thus increases in secondary production of herbivores may occur following clearcutting, but there may be declines in secondary production of detritivores.

Vertebrate Predators

The immediate effects of logging and road building frequently cause fish populations to decline, a response that may be related to loss of habitat, decreased habitat stability, high rates of sedimentation, low concentrations of dissolved oxygen, and elevated water temperatures. Generally, the duration of these effects is limited to less than ten years after logging, frequently only a year or two. Within a basin, however, the cumulative effects of these factors may be much more persistent.

Habitats are physically restructured by entry of machinery and felling of trees into stream channels, occurring both intentionally and unintentionally. Distribution and dimensions of riffles, pools, side channels, and eddies are changed, and populations of both aquatic invertebrates and fish are adversely affected. Not only do populations decline, but the age structure and species composition may shift. Removal of coarse woody debris exacerbates this problem. Such channel changes also affect the relative stability of channel morphology and stream substrates. Lateral habitats (e.g., side channels, backwaters, eddies), which provide critical rearing habitat for salmonid fry, are less persistent over the year and therefore are less predictable habitats. Fish populations can potentially adjust to the shifts in habitat distributions and, to a lesser degree, changes in habitat dimensions, but the persistent instability of habitat makes reestablishment of stable populations impossible.

Habitat alteration is compounded by increased loading of sediments into streams during and after logging. The sediments can fill the interstitial spaces within the streambed, blanket the surface of the streambed, fill pools and backwaters, elevate riffles, and deposit onto floodplains. As a result, surface habitats and intragravel habitats for invertebrates, fry, and adult salmonids are lost. Sedimentation covers spawning gravels, reducing potential spawning area and increasing the mortality of eggs and fry because of decreased subsurface flow, decreased oxygen concentrations, and physical blockage to emergence from the gravel. Generally, erosional inputs are composed of particles smaller than the average particle in the channel; therefore the overall stability of substrates at high flow is reduced.

Increases in stream temperature often accompany canopy removal. Elevated water temperature can directly increase the mortality of fish, and it can cause changes in community structure and increase competition between species. All organisms can tolerate a range of temperatures, and this range can differ slightly for different populations. If the thermal regime of a particular stream exceeds the tolerance range for a species, populations will decline; therefore, populations in streams in areas on the warmer end of the range of a species are more vulnerable to the deleterious effects of increased water temperature. In southern Ontario, trout populations were sparse in streams with weekly maximum water temperatures in excess of 22°C (Barton et al. 1985). Variation in maximum stream temperatures was explained by the percentage of streambank that was forested above these sites. Populations in cooler regions may even benefit from such changes. A more subtle influence of temperature changes is the potential shift in fish community structure. Temperature may either enhance or decrease the survival of other species, thereby changing the relative abundance or the number of species in a stream. Competition between populations may decrease the growth and survival of species of interest.

The deleterious effects of forest practices on fish populations are frequently emphasized, but logging can also enhance fish populations. Many studies have found greater numbers and larger fish in open reaches of streams in logged watersheds (Hall and Lantz 1969, Aho 1977, Murphy and Hall 1981, Murphy et al. 1981, Tschaplinski and Hartman 1983). These increases generally occur after channels have restabilized to some degree and erosional inputs have diminished. Such increases may be attributable to increased food availability and greater efficiency of prey capture. As described earlier, increased solar radiation results in greater primary production and greater abundance of mayflies and midges, invertebrates that are generally considered to be behavioral drifters. Because most stream salmonids are drift feeders, these changes may result in greater prey availability. Analysis of stomach contents of salmonids in these areas supports this interpretation (Aho 1977). This response to logging is further enhanced by the increased efficiency with which trout and salmon are able to capture their food. As light intensity increases, salmonids are better able to distinguish prey items in the water column and to capture items in the drift (Wilzbach et al. 1986). As a result, their growth and survival potentially increase. Other factors that potentially play a role in population increases after logging include habitat diversity and increased temperature, but no investigations have demonstrated such influences.

Sedimentation may have adverse effects on fish populations in many streams, but in sediment-poor streams it may represent a critical source of substrates for habitat and spawning. Many streams, particularly in the Coast Range of the Pacific Northwest, are dominated by extensive bedrock reaches that offer little habitat for invertebrates or fish. Landslides and surface erosion may deliver much-needed sediment to the reaches. Large roughness elements such as boulders and logs are essential for stabilizing these extensively eroded sections of a drainage. In Knowles Creek, a coastal stream in Oregon, densities of coho salmon

were highest in the depositional reaches of debris torrents (Everest and Meehan 1981). These torrents provided boulders, cobble, and gravel in a stream that was dominated by long reaches of bedrock. In such cases, landslides may have positive influences on fish populations.

Summer is a relatively benign period of survival for most populations of salmon, trout, and other species, but winter floods are critical times for any fish populations. The stability of habitats, especially lateral or off-channel habitats, is extremely crucial, because these areas serve as refuges during floods. Coarse woody debris plays a major role in winter habitat. Enhanced production that may occur during summer may be negated by decreased overwinter survival. In southeastern Alaska, densities of juvenile salmonid fry were examined in streams in old-growth forests, streams in clearcuts, and streams in clearcuts but with buffer strips of intact riparian vegetation (Koski et al. 1984). As a result of extensive blow down, the buffered reaches exhibited the highest standing crops of woody debris; the clearcuts had been cleaned of woody debris after logging and exhibited the lowest standing crops of woody debris. Densities of coho fry were significantly higher in the clearcut and buffered reaches than in the reaches in old-growth forests. The densities of coho parr were highest in the buffered reaches, intermediate in the old-growth forest reaches, and lowest in the clearcut reaches. Coho salmon spend two years in these Alaskan streams before they migrate to the ocean, therefore parrs are one year old and represent that portion of the population that survived through winter. Algal biomass and invertebrate densities were greatest in the open reaches in summer. These data indicate that the reaches with greater solar radiation reaching the stream support more fish during summer, but survival through winter is greatest in those streams with more stable habitat and refuge at high flow. The responses of coho salmon observed in the southeastern Alaskan streams were consistent with results of attempts to increase production of stream salmonids in British Columbia. Mason (1976) found that availability of winter habitat nullified increases in a coho salmon population created by artificial food supplementation during summer.

No single factor is sufficient to determine the production of fish populations in streams. Both habitat and food resources are major determinants of the survival and production of fish in streams, but they are both composed of a complex array of factors that vary spatially and temporally in importance. Fish populations may be limited by the availability of food during one part of the year and by habitat during another, as in the Alaskan streams. Limitations to fish production may also vary spatially. Nutritional resources and physical habitat shift from headwaters to large rivers (Vannote et al. 1980), therefore factors that determine the survival and production of fish may also vary within a drainage. Although it is always tempting to seek simple answers to complex problems, appropriate management of natural resources must incorporate the natural complexity and variability of terrestrial ecosystems.

TEMPORAL PATTERNS OF BIOTIC RESPONSES

Revegetation of riparian zones following timber harvest, or any event that removes riparian vegetation (e.g., wildfire, wind throw, landslides, debris torrents), usually follows a predictable sequence of successional changes (Figure 4). Riparian zone revegetation is initiated by regrowth of herbaceous plants through seed germination or resprouting from residual plant parts. Herbaceous species typically reestablish within a year after logging and reach their maximum abundance and productivity within five years after harvest. Regrowth of shrubs and young deciduous trees begins within five years following harvest. Deciduous species (e.g., alder) dominate a riparian corridor approximately thirty to forty years after harvest. At this time, shading of riparian zones by the deciduous canopy results in reduction in abundance and dominance by herbs and shrubs in streamside areas. Deciduous tree species begin to die off at forty to eighty years of age and slow-growing coniferous trees (e.g., fir, hemlock, cedar, spruce) begin to dominate riparian zones at this time. Conifers reach their maximum size and abundance at time scales greater than 150 years after harvest, assuming that no major resetting disturbance occurs during that interval. Input of large woody debris to streams begins with the death of individual conifers in riparian zones more than 200 years after harvest. Maximum loading of woody debris to streams occurs within this time frame.

Removal of riparian vegetation in forested ecosystems results in increases in light energy to streams (Figure 5). Light intensities reaching the stream remain high for up to ten years after harvest and decline with canopy closure over streams by deciduous tree species. Light intensities are lowest during the ten to one hundred year period of dominance by deciduous species. Input of solar radiation may increase slightly with subsequent declines in deciduous species and increases in conifers. Nutrient concentrations, particularly inorganic nitrogen, usually increase within a short time after harvest because of increases in overland runoff and soil erosion that contribute unbound (e.g., nitrate, ammonium) and bound (orthophosphate) nutrients to the stream. In addition, leaching and decomposition of logging slash left in the stream or riparian zone can contribute large amounts of dissolved organic carbon to the stream. Nutrient inputs to the stream should decline as regrowth of riparian vegetation and soil stabilization result in lower rates of erosion and runoff. Habitat and substrate stability will be low in initial periods following harvest; this instability will persist until geomorphic surfaces in riparian zones are revegetated. Substrate and habitat stability is maximized at periods greater than a century after harvest, when dominant conifer stands contribute coarse woody debris to stream channels.

Productivity of stream microorganisms is highly influenced by light, nutrient, and substrate conditions (Figure 6). Rates of primary production are influenced by light, nutrients, current velocity, sediment, grazing, and disturbance. Increased light and nutrient levels immediately following timber harvest can elicit increased primary production that may persist for ten to twenty years. As deciduous tree growth results in increased canopy closure (i.e., light levels decline)

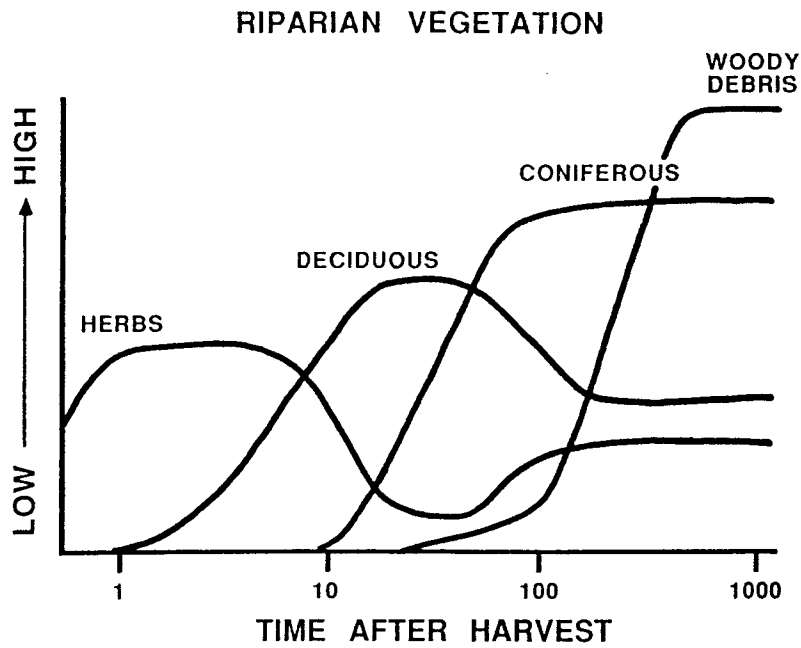


Figure 4. Temporal patterns of relative dominance of riparian vegetation after timber harvest (time is expressed as years on a logarithmic scale).

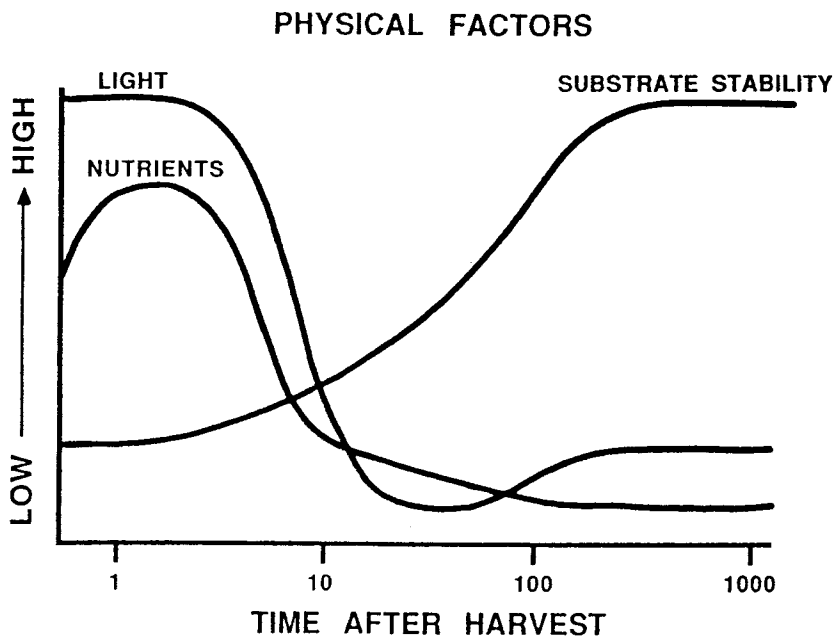


Figure 5. Temporal patterns of relative amounts of solar radiation and nutrients and the degree of substrate stability after timber harvest (time is expressed as years on a logarithmic scale).

STREAM MICROORGANISMS

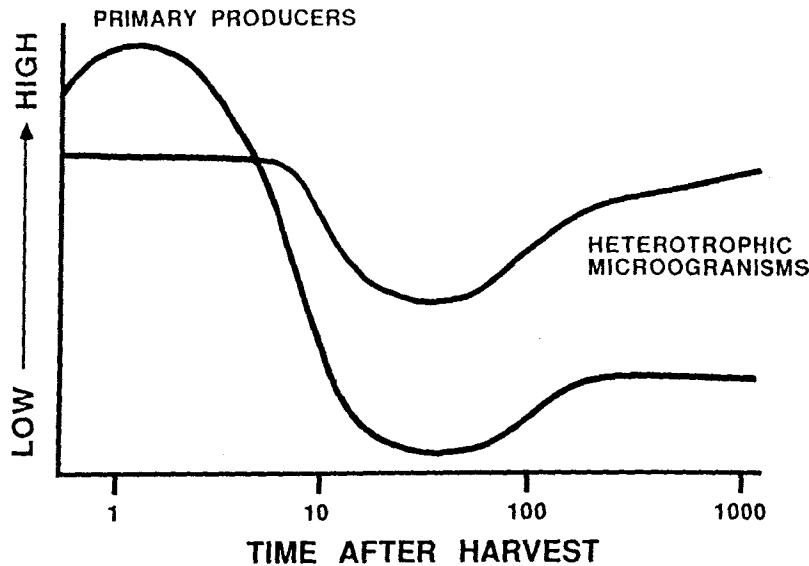


Figure 6. Temporal patterns of relative abundances of aquatic primary producers and heterotrophic microorganisms in streams after timber harvest (time is expressed as years on a logarithmic scale).

and nutrient levels fall, rates of primary production will decline to a minimum during dominance by the deciduous community forty to eighty years after logging. Heterotrophic (microbial) activity will be high shortly after harvest because of high levels of particulate organic carbon (e.g., logging slash, algae) and dissolved organic carbon in the stream. Inputs of readily decomposable herbaceous detritus within the first decade after clearcutting will maintain high levels of heterotrophic activity during that period. Heterotrophic activity should decline somewhat after forty to eighty years, prior to major inputs of coarse woody debris. Resumption of woody debris inputs after a century or more will result in greater storage of organic matter and increased heterotrophic activity.

Different trophic feeding groups of macroinvertebrates will show different responses to the availability of food resources in the chronological sequence following harvest (Figure 7). Herbivorous invertebrates will be most abundant in the initial period following harvest when algal production is highest. This abundance may be maintained for up to ten years after logging, but will be most pronounced for the first two to three years. Detritivorous invertebrates may respond quickly to detrital loading by logging slash, but abundances will generally be low in the initial ten years, because food availability will be weighted toward primary producers. With a shift in the composition of food resources within the first century toward increasing allochthonous inputs (herbaceous and deciduous detritus) and declining autotrophic production (primarily algae), there will be a shift in invertebrate trophic composition toward higher abundances of

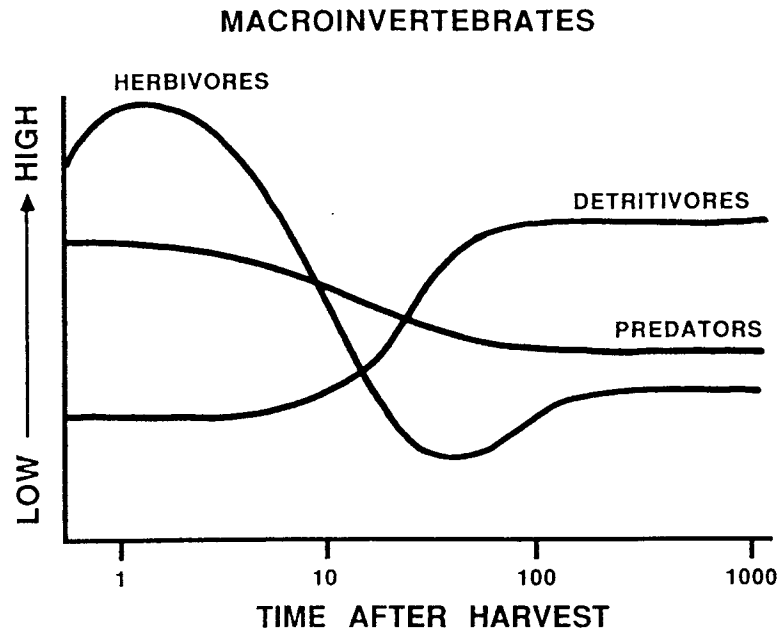


Figure 7. Temporal patterns of relative densities of macroinvertebrate communities in streams after timber harvest (time is expressed as years on a logarithmic scale).

detritivores and lower numbers of herbivores. Predators will not show marked shifts in abundance, because they prey on both detritivores and herbivores, but may respond positively to high herbivore densities during the initial period following harvest.

The responses described above must be viewed in the context of a sliding time scale. These changes and responses may be compressed into a shorter period or expanded into a longer one depending on such features of the watershed as site productivity, climatic regime, geology, geomorphology, and availability of biological inocula for aquatic and terrestrial habitats. In general, aquatic community production (primary and secondary) will tend to increase in the initial period following harvest, but community stability will be low (Figure 8). Disturbance of the stream habitat will be high and biological communities will show little resistance to such perturbation. However, communities may recover rapidly from such disturbance (high resilience). After longer periods of time, aquatic production will decline but habitat and community stability will increase. Physical and biological attributes of the stream will be more resistant to disturbance, but recovery periods from perturbation may be long (low resilience).

MANAGEMENT OBJECTIVES FOR AQUATIC RESOURCES

Management of aquatic resources in forested landscapes requires that we clearly state achievable objectives for that management. We, as fishery biologists, have been extremely vague and reluctant in defining

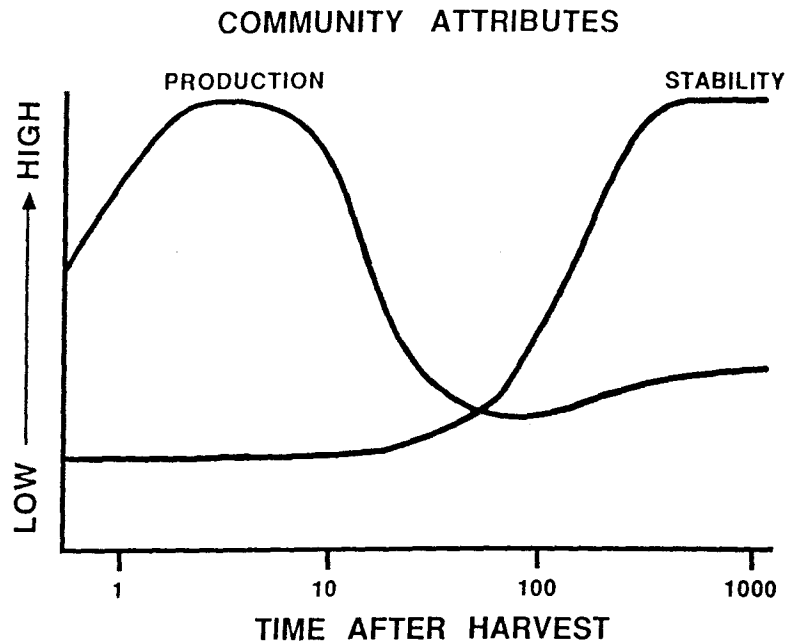


Figure 8. Temporal responses of the total production and stability of aquatic communities in streams after timber harvest (time is expressed as years on a logarithmic scale).

such objectives. We often refer to such concepts as the "health" of the stream, but how do we evaluate the "health" of streams? Often there are two unstated objectives implicit in the concern about forest practices on fisheries in streams. One is that the fishery (stream system) will be unaffected by timber harvest operations. This objective is logically related to regulations and harvest performance standards near streams that are designed for "no change" in the stream system. The second, usually dominant, objective is to maximize the productivity of fish populations. But do we really want to base our management of fisheries on productivity alone? Many aquatic ecosystems are extremely productive but would not be desirable management objectives (e.g., Lake Erie, sewage lagoons, etc.). Streams in harvested watersheds may be more productive under certain circumstances, but the abundance and distribution of organisms in these streams may fluctuate more than those in streams in mature forests. In other words, we have a trade-off between productivity and persistence. If short-term productivity is our sole criterion for management, we may sacrifice long-term stability of aquatic ecosystems.

Streams in the Pacific Northwest frequently contain two to four species of salmonids in addition to nonsalmonids. Short-term increases in one species can be viewed as a positive response, yet the long-term stability of even this species is linked to the dynamics of other fish populations. The productivity of one species potentially affects the total productive output of all species. In many instances, management of streams is designed to enhance populations of anadromous salmonids, even to the detriment of other native fishes, including native salmonids.

Long-term management of fishery resources must ensure the integrity of all fish stocks.

In evaluating the effects of forest practices, we must eventually address the recovery of stream ecosystems. But what do we mean by "recovery"? Recovery is frequently measured in terms of taxonomic composition, species diversity, composition of functional groups, various biological processes, and physical structure. All of these characteristics of stream ecosystems are important aspects of recovery, but any single factor alone is insufficient to evaluate recovery. Streams may never actually recover to the original state, either physically or biologically. Recovery may require extremely long periods. In northern California, invertebrate densities in streams with no buffer strips in logged watersheds were still lower than those in nearby streams in old-growth watersheds ten years after logging (Erman and Mahoney 1983). It is theoretically possible that if a system is greatly altered for a long enough period, cessation of the altering forces does not result in recovery to the initial predisturbed state. Instead, the new community of organisms and altered ecosystem functions (such as productivity or organic matter processing) remain. For the manager, then, restoration of the previous stream system may not be achieved merely by halting disturbance. Rather, substantial energy and precise knowledge of reactions must be employed to return the system--a task that may exceed current levels of understanding or financial support.

Characteristics of terrestrial and aquatic ecosystems are determined by the interaction of the physical factors and biological communities. It is obvious that the physical environment strongly influences biological communities, but it is also apparent that living organisms greatly modify the physical environments of stream ecosystems. Sediment routing, water temperature, nutrient dynamics, landslides, humidity, concentrations of atmospheric gases, precipitation, streamflow, and many other "physical factors" are strongly influenced by living organisms. Riparian zones and the aquatic ecosystems within them are created and maintained by these interactions between physical processes and biological communities.

The landscapes and biotic communities of terrestrial and aquatic ecosystems are intricately linked, and forest practices potentially alter these linkages. We must adopt rigorous concepts of riparian zones that encompass the many linkages between these ecosystems. Land use managers in the Pacific Northwest face an intimidating array of ever-changing issues. There are no easy answers. There is no panacea. Effective management of riparian zones to minimize changes in aquatic ecosystems must acknowledge and incorporate the complexity and variability of natural systems. Appropriate management systems that take advantage of existing knowledge and identify critical areas for investigation require active cooperation, and communication between land managers, ecologists, physical scientists, and the public.

LITERATURE CITED

- Aho, R. S. 1977. A population study of the cutthroat trout in an unshaded and shaded section of stream. M.S. thesis, Oregon State University, Corvallis. 87 p.
- Barton, D. R., W. D. Taylor, and R. M. Biette. 1985. Dimensions of riparian buffer strips required to maintain trout habitat in southern Ontario streams. *North Am. J. Fish. Manage.* 5:364-378.
- Brown, G. W., and J. T. Krygier. 1970. Effects of clearcutting on stream temperature. *Water Resour. Res.* 6:1133-1139.
- Busch, D. E. 1978. Successional changes associated with benthic assemblages in experimental streams. Ph.D. thesis, Oregon State University, Corvallis. 91 p.
- Cummins, K. W. 1974. Stream ecosystem structure and function. *BioScience* 24:631-641.
- Cummins, K. W., J. R. Sedell, F. J. Swanson, G. W. Minshall, S. G. Fisher, C. E. Cushing, R. C. Petersen, and R. L. Vannote. 1982. Organic matter budgets for stream ecosystems: Problems in their evaluation. *In* G. W. Minshall and J. R. Barnes (eds.) *Stream ecology: Application and testing of general ecological theory*, p. 299-353. Plenum Press, New York.
- Dever, J. E. 1962. Plant production in a woodland stream under controlled conditions. M.S. thesis, Oregon State University, Corvallis. 62 p.
- Erman, D. C., and D. Mahoney. 1983. Recovery after logging in streams with and without bufferstrips in northern California. Contribution 186. California Water Resources Center, University of California, Davis. 50 p.
- Erman, D. C., J. D. Newbold, and K. B. Roby. 1977. Evaluation of streamside bufferstrips for protecting aquatic organisms. Contribution 165. California Water Resources Center, University of California, Davis. 448 p.
- Everest, F. H., and W. R. Meehan. 1981. Forest management and anadromous fish habitat productivity. Transactions of the 46th North American Wildlife and Natural Resources Conference, p. 521-530.
- Fisher, S. G., and G. L. Likens. 1973. Energy flow in Bear Brook, New Hampshire: An integrative approach to stream ecosystem metabolism. *Ecol. Monogr.* 43:421-439.
- Fredriksen, R. L. 1971. Comparative water quality: Natural and disturbed streams. *In* J. T. Krygier and J. D. Hall (eds.) *Forest land uses and stream environment: Proceedings of a symposium*, p. 125-137. Oregon State University, Corvallis.
- Gregory, S. V. 1980. Effects of light, nutrients, and grazing on periphyton communities in streams. Ph.D. thesis, Oregon State University, Corvallis. 151 p.
- Hall, C. A. S. 1972. Migration and metabolism in a temperate stream ecosystem. *Ecology* 53:585-604.
- Hall, J. D., and R. L. Lantz. 1969. Effects of logging on the habitat of coho salmon and cutthroat trout in coastal streams. *In* T. G. Northcote (ed.) *Symposium on Salmon and Trout in Streams*, p. 355-375. H. R. MacMillan Lectures in Fisheries. University of British Columbia, Vancouver.
- Hansmann, E. W., and H. K. Phinney. 1973. Effects of logging on periphyton in coastal streams of Oregon. *Ecology* 54:194-199.
- Hawkins, C. P., M. L. Murphy, and N. H. Anderson. 1982. Effects of canopy, substrate composition, and gradient on the structure of macroinvertebrate communities in Cascade Range streams of Oregon. *Ecology* 63:1840-1856.

- King, D. K. 1983. Community metabolism and autotrophic-heterotrophic relationships of woodland stream riffle sections. Ph.D. thesis, Michigan State University. 356 p.
- Koski, K V., J. Heifetz, S. Johnson, M. Murphy, and J. Thedinga. 1984. Evaluation of buffer strips for protection of salmonid rearing habitat and implications for enhancement. *In* T. J. Hassler (ed.) Proceedings: Pacific Northwest Stream Habitat Management Workshop, p. 138-155. Humboldt State University, Arcata, California.
- Lamberti, G. A., and J. W. Moore. 1984. Aquatic insects as primary consumers. *In* V. H. Resh and D. M. Rosenberg (eds.) The ecology of aquatic insects, p. 164-195. Praeger Science, New York.
- Lamberti, G. A., and V. H. Resh. 1983. Stream periphyton and herbivores: An experimental study of grazing by a caddisfly population. *Ecology* 64:1124-1135.
- Likens, G. E., F. H. Bormann, N. M. Johnson, D. W. Fisher, and R. S. Pierce. 1970. Effects of forest cutting and herbicide treatment on nutrient budgets in the Hubbard Brook watershed-ecosystem. *Ecol. Monogr.* 40:23-47.
- Mason, J. C. 1976. Response of underyearling coho salmon to supplemental feeding in a natural stream. *J. Wildl. Manage.* 40:775-788.
- Meehan, W. R., F. J. Swanson, and J. R. Sedell. 1977. Influences of riparian vegetation on aquatic ecosystems with particular references to salmonid fishes and their food supply. *In* R. R. Johnson and D. A. Jones (eds.) Importance, preservation and management of riparian habitat: A symposium. USDA For. Serv. Gen. Tech. Rep. RM-43. Rocky Mountain For. and Range Exp. Stn., Fort Collins, Colorado.
- Minshall, G. W., R. C. Petersen, K. W. Cummins, T. L. Bott, J. R. Sedell, C. E. Cushing, and R. L. Vannote. 1983. Interbiome comparison of stream ecosystem dynamics. *Ecol. Monogr.* 53:1-25.
- Murphy, M. L., and J. D. Hall. 1981. Varied effects of clear-cut logging on predators and their habitat in small streams of the Cascade Mountains, Oregon. *Can. J. Fish. Aquat. Sci.* 38:137-145.
- Murphy, M. L., C. P. Hawkins, and N. H. Anderson. 1981. Effects of canopy modification and accumulated sediment on stream communities. *Trans. Am. Fish. Soc.* 110:469-478.
- Naiman, R. J., and J. R. Sedell. 1980. Relationships between metabolic parameters and stream order in Oregon. *Can. J. Fish. Aquat. Sci.* 37:834-847.
- Newbold, J. D., D. C. Erman, and K. B. Roby. 1980. Effects of logging on macroinvertebrates in streams with and without buffer strips. *Can. J. Fish. Aquat. Sci.* 37:1076-1085.
- Petersen, R. C., and K. W. Cummins. 1974. Leaf processing in a woodland stream. *Freshw. Biol.* 4:343-368.
- Phinney, H. K., and C. D. McIntire. 1965. Effect of temperature on metabolism of periphyton communities developed in laboratory streams. *Limnol. Oceanogr.* 10:341-344.
- Rounick, J. S., and S. V. Gregory. 1981. Temporal changes in periphyton standing crop during an unusually dry winter in streams of the western Cascades, Oregon. *Hydrobiologia* 83:197-205.
- Sedell, J. R., F. J. Triska, and B. M. Buckley. 1975. The processing of coniferous and hardwood leaves in two coniferous forest streams. Part 1: Weight loss and associated invertebrates. *Verh. Int. Ver. Limnol.* 19:617-627.

- Speaker, R. 1985. Distribution and retention of particulate organic matter in streams in the Cascade Mountains of Oregon. M.S. thesis, Oregon State University. 145 p.
- Speaker, R., K. Moore, and S. Gregory. 1984. Analysis of the process of retention of organic matter in stream ecosystems. *Verh. Int. Ver. Limnol.* 22:1835-1841.
- Speir, J. A. 1979. Energy transfer in an autotrophic-based stream ecosystem with special reference to effects of fertilizer nitrogen additions. *Bull.* 9. Coniferous Forest Biome, Ecosystem Analysis Studies, College of Forest Resources, University of Washington, Seattle.
- Stockner, J. G., and K. R. S. Shortreed. 1976. Autotrophic production in Carnation Creek, a coastal rainforest stream on Vancouver Island, British Columbia. *J. Fish. Res. Board Can.* 33:1553-1563.
- Sumner, W. T., and S. G. Fisher. 1979. Periphyton production in Fort River, Massachusetts. *Freshw. Biol.* 9:205-212.
- Sumner, W. T., and C. D. McIntire. 1982. Grazer-periphyton interactions in laboratory streams. *Archiv für Hydrobiologie* 93:135-157.
- Swanson, F. J., S. V. Gregory, J. R. Sedell, and A. G. Campbell. 1982. Land-water interactions: The riparian zone. *In* R. L. Edmonds (ed.) *Analysis of coniferous forest ecosystems in the western United States.* Hutchinson Ross Publishing Co., Stroudsburg, Pennsylvania.
- Thut, R. N., and E. P. Haydu. 1971. Effects of forest chemicals on aquatic life. *In* J. T. Krygier and J. D. Hall (eds.) *Forest land uses and stream environment: Proceedings of a symposium,* p. 159-171. Oregon State University, Corvallis.
- Triska, F. J., F. C. Kennedy, R. J. Avanzino, and B. N. Reilly. 1983. Effect of simulated canopy cover on regulation of nitrate uptake and primary production by natural periphyton assemblages. *In* T. D. Fontaine III and S. M. Bartell (eds.) *Dynamics of lotic ecosystems,* p. 129-159. Ann Arbor Science, Michigan.
- Triska, F. J., J. R. Sedell, and S. V. Gregory. 1982. Coniferous forest streams. *In* R. L. Edmonds (ed.) *Analysis of coniferous forest ecosystems in the western United States,* p. 292-332. Hutchinson Ross Publishing Co., Stroudsburg, Pennsylvania.
- Tschaplinski, P. J., and G. F. Hartman. 1983. Winter distribution of juvenile coho salmon (*Oncorhynchus kisutch*) before and after logging in Carnation Creek, British Columbia, and some implications for overwinter survival. *Can. J. Fish. Aquat. Sci.* 40:452-461.
- Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. The river continuum concept. *Can. J. Fish. Aquat. Sci.* 37:130-137.
- Wilzbach, M. A., K. W. Cummins, and J. D. Hall. 1986. Influence of habitat manipulations on interactions between cutthroat trout and invertebrate drift. *Ecology* 67:898-911.