

Chapter 6

AQUATIC ECOSYSTEMS OF THE REDWOOD REGION

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The primary purpose of this chapter is to describe aquatic ecosystems within the redwood region and discuss related management and conservation issues. Although scientists from many disciplines have conducted research in the redwood region, few comprehensive interdisciplinary studies exist (but see Zieman 1998b) and no regionwide overview or synthesis of the aquatic systems in the redwoods has been published. Private ownership of most of the region has limited access and, therefore, scientific study in many areas. Fortunately, a large body of applicable science exists on riparian and aquatic systems and the relationships between geomorphological, hydrologic, and biotic processes in the Pacific Northwest, some inclusive of the redwood region (e.g., Meehan 1991; Spence et al. 1996; National Research Council 1996; Stouder et al. 1997).

The redwood forests are in the coast range ecoregion (Omernik and Gallant 1986), mainly in northern California. Coastal streams with basins of 60-80 km² (e.g., Redwood Creek) may be entirely within the redwood zone, but the larger

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rivers (e.g., Russian, Eel, Mad, Klamath, and Smith Rivers) flow through the redwood zone only in their lowermost sections, with headwaters well inland from the coast and the redwood belt. The influence of redwoods on stream communities, therefore, is more pronounced in the small coastal streams than in larger rivers. Smaller streams also are more directly linked to and influenced by the adjacent riparian plant community. For this reason, the primary focus of this chapter is on the relatively small streams that originate and enter the ocean within the coastal redwood zone, although we do reference relevant research from the larger riverine systems that transect the redwood region.

Our approach here is, first, to discuss in some detail the structures and processes, and the spatial and temporal dynamics, that constitute a healthy riparian/aquatic ecosystem in the redwood region. This perspective is critical to understanding the ecological and evolutionary context within which the aquatic and riparian species of the redwoods have evolved over the millennia. This background also provides the appropriate frame of reference for discussing recent anthropogenic changes resulting from timber harvesting, road building, and other activities.

Stream Ecosystem Processes in Pristine Watersheds

Although few watersheds in the redwood region are pristine today, some understanding of how unaltered watersheds function is necessary to guide conservation and restoration programs. Here, we discuss the roles of riparian vegetation and large woody debris in streams, the river continuum concept, stream responses to catchmentwide processes, and the role of disturbance in stream ecosystems.

The Role of Riparian Vegetation and Large Woody Debris

Riparian plants play a dominant role in stream ecosystems. Terrestrial plants provide shade, regulate microclimates, and contribute both large wood pieces that add habitat complexity and small organic materials that serve as food for aquatic organisms. They also stabilize stream banks, control sediment inputs from surface erosion, and regulate nutrient and pollutant inputs (fig. 6.1; Gregory et al. 1991; Naiman et al. 1992; Spence et al. 1996; Naiman and Decamps 1997; Naiman et al. 1998). Redwood trees, by their size, age, and resistance to fire, floods, and decomposition, play a central role in shaping the physical and chemical conditions within the aquatic zone and thereby strongly affect the aquatic community. Among the world's tallest trees, redwoods cast long shadows and shade even wide streams. Large redwoods entering streams as a result of blowdown, bank undercutting, or mass wasting can remain there for centuries, functioning as stream features that rival bedrock sills or outcrops in regulating channel processes. Historical harvesting of redwoods throughout

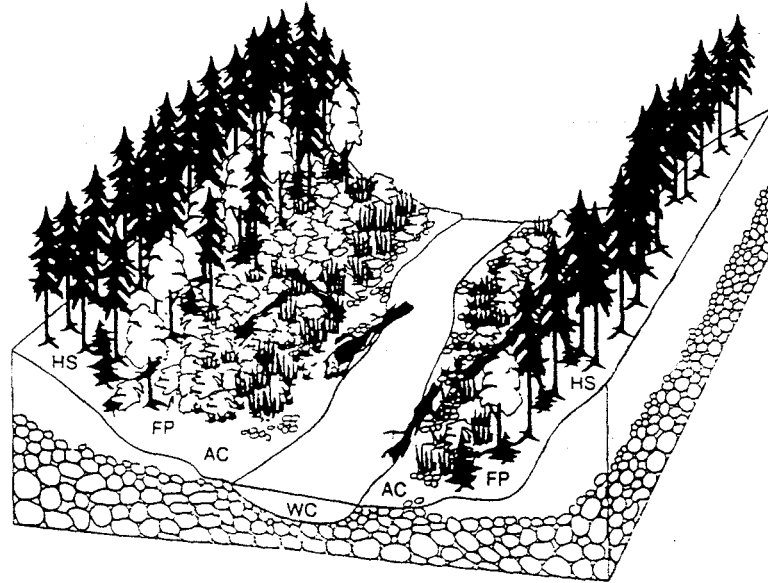


Figure 6.1. Typical patterns of riparian plant communities associated with different geomorphic surfaces of river valleys in the Pacific Northwest. Scattered patches of grasses and herbs occur on exposed portions of the active channel (AC), but little terrestrial vegetation is found within the low-flow wetted channel (WC). Floodplains (FP) include mosaics of herbs, shrubs, and deciduous trees. Conifers are scattered along floodplains and dominate older surfaces. The overstory species in riparian forests on lower hillslopes (HS) consist primarily of conifers. (From Gregory et al. 1991.)

most of the region, however, with much of the early harvest taking place along streams, has significantly altered stream ecosystems. Current harvesting is often still focused around streams because trees grow larger and more quickly there.

Stream channels in pristine watersheds exhibit a complex array of hydraulic conditions (pools, riffles, alcoves, side channels, single and multiple channel sections), substrate sizes, and accumulations of wood and other organic matter. Woody debris is one of five watershed elements that create and modify stream habitats, the others being water, sediments, nutrients, and heat (table 6.1; Naiman et al. 1992). Large woody debris consists of large logs that fall into stream channels, either from natural tree death, windthrow, or bank failure, and then play a central role in structuring stream habitats (table 6.1; Sedell et al. 1988). In the redwood region, large redwood logs can have a dominant influence on stream processes and channel complexity (Keller et al. 1995). In headwater streams flowing through old-growth redwoods, nearly all pools are either formed directly or influenced significantly by large organic debris (i.e., logs) (Keller et al. 1995). Welsh and Ollivier (unpub. data) reported an average

Table 6.1. Riparian Forests: Important Ecological Elements and Their Functions for Aquatic and Riparian Vertebrate and Invertebrate Communities.

<i>Location and Function</i>	<i>Element</i>						
	<i>Large Woody Debris</i>	<i>Organic Litter</i>	<i>Roots</i>	<i>Substrate</i>	<i>Overstory Vegetation</i>	<i>Understory Vegetation</i>	<i>Soil</i>
STREAM CHANNEL							
Provides breeding, feeding, and shelter habitat for many species	X	X	-	X	X	X	-
Controls aquatic habitat dynamics	X	-	-	-	-	-	-
Contributes to formation of islands and floodplains	X	-	-	-	-	-	-
Sort, routes, and retains substrates	X	-	-	-	-	-	-
Filters and stores sediments and organic material	X	-	-	-	-	-	-
Increases primary and secondary production	-	X	-	-	-	-	-
Self sorts and provides habitat heterogeneity	-	-	-	X	-	-	-
STREAM BANKS							
Provides breeding, feeding, and shelter habitat for many species	X	-	X	X	X	X	X
Stabilizes stream banks	X	-	X	-	-	-	-
Provides coarse, woody debris to channel	X	-	-	-	-	-	-
Provides substrate to channel	-	-	-	X	-	-	-
FLOODPLAIN							
Provides breeding, feeding, and shelter habitat for many species	X	X	-	X	X	X	X

<i>Location and Function</i>	<i>Element</i>						
	<i>Large Woody Debris</i>	<i>Organic Litter</i>	<i>Roots</i>	<i>Substrate</i>	<i>Overstory Vegetation</i>	<i>Understory Vegetation</i>	<i>Soil</i>
Regulates air temperature, humidity, and solar penetration	-	-	-	-	X	X	-
Provides suitable microclimatic conditions	X	X	-	X	-	-	-
Provides woody debris to channel	X	-	-	-	X	-	-
Provides organic litter to channel	-	-	-	-	X	X	-
Retards movement of coarse woody debris	-	-	-	-	X	X	-
Filters sediment	X	X	-	X	X	X	-
Dissipates water Energy	X	X	-	X	X	X	-
ADJACENT HILLSLOPE							
Provides breeding, feeding, and shelter for many species	-	-	-	-	X	X	-
Regulates air temperature, humidity, and solar penetration	-	-	-	-	X	X	-
Provides coarse, woody debris to floodplain and channel	X	-	-	-	X	-	-
Provides organic litter to floodplain and channel	-	X	-	-	X	X	-
Protects riparian forest from effects of wind	-	-	-	-	X	X	-
Provides recruitment source to floodplain and channel	-	-	-	X	-	-	-
Filters sediment	X	X	-	-	X	X	-
Dissipates water energy	X	X	-	-	X	X	X

of 55 logs > 50 cm dbh/km (S. D. 11) for 10 streams in an old-growth redwood forest in Prairie Creek Redwoods State Park (Humboldt Co.); 99 percent were conifer logs, primarily redwood. Keller et al. (1995) aged 30 individual logs in the Prairie Creek Basin and found about half of them to have been in the stream for more than 100 years, some in excess of 200 years. In coastal Oregon streams, 70 percent of pools > 1 m³ in volume were formed by wood (Andrus 1988). Andrus also noted that conifers are markedly more decay-resistant than hardwoods, and that redwood and cedar logs outlast Douglas-fir and hemlock logs in streams. In a natural system with intact riparian forests, a large proportion of these logs would enter streams from the highest channels in the stream network (i.e., the first-order channels; Strahler [1957]) during large storm events (Sedell et al. 1988). Because they provide large woody debris and a variety of sediment types, headwater or first-order stream channels strongly influence the type and quality of downstream fish habitat (Sedell et al. 1988). Stated succinctly, "Reaches that are themselves inhospitable to salmonids may contribute to the maintenance of salmonid populations downstream" (G. Reeves in Reid 1998).

The River Continuum Concept

The river continuum concept (fig. 6.2; Vannote et al. 1980; Minshall et al. 1983, 1985, 1992) describes the changes natural stream communities undergo from headwater areas to lower elevations in response to riparian and fluvial processes. Relative contributions of energy from riparian versus aquatic primary producers (plants), and the size and type of organic material transported from upstream areas, change predictably through the progression from headwaters to the mouth in natural stream communities. Small headwater streams have steep gradients, confined channels, and cool temperatures when adequately shaded by riparian vegetation. Consequently, they obtain most of their organic material in the form of leaves, needles, branches, and other plant parts from the riparian zone rather than from primary producers within the stream. Farther down the river continuum, stream channels are less confined and have more extensive floodplains. Instream primary production increases in response to greater light penetration. Daily temperature fluctuations in these lower stream sections also are more pronounced because of increased exposure to solar warming (Beschta et al. 1987). Historically, the presence of old-growth redwoods and a low level of forest disturbance in the riparian zone of small and intermediate-size streams resulted in extensively shaded streams with limited temperature gains and primary production (table 6.1). Large woody debris input also changes along the stream continuum, with smaller channels contributing more large woody debris to the stream network than larger channels (Sedell et al. 1988).

Biological communities in streams are highly complex and dynamic entities comprising hundreds of plant and animal species structured and organized in

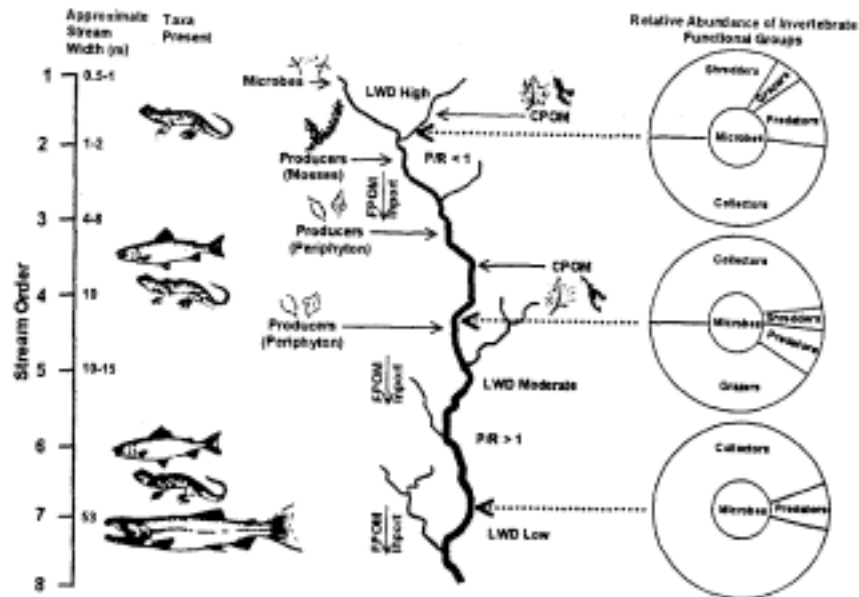


Figure 6.2. The river continuum concept (adapted from Vannote et al. 1980). An example showing stream width, dominant predators, producer groups, production (P) to respiration (R) ratios, importance of wood, and proportions of invertebrate functional groups. CPOM = coarse particulate organic matter, FPOM = fine particulate organic matter. (Adapted from Sedell et al. 1988.)

response to physical, chemical, and biological interactions. Interactions among the major abiotic factors (solar energy, climate, geology, geomorphology, and hydrology) provide the physical environment (Bencala 1984; Boulton and Lake 1991) that influences the species composition of the community. Biological interactions between organisms include food-web linkages (e.g., herbivory, predator-prey), competition, mutualism, and disease-host or parasite-host relationships (Spence et al. 1996). Energy flow within stream communities is often represented by the feeding relationships of these functional groups (table 6.2; fig. 6.2). The base of the food web is provided by plants, either from the riparian zone (allochthonous material) or instream primary producers (autochthonous material), such as algae, mosses, and rooted aquatic vascular plants.

The river continuum concept (Vannote et al. 1980) predicts a systematic change in consumer functional groups from headwater areas downstream (table 6.2; fig. 6.2). Small streams are dominated by invertebrates (shredders and collectors) that process riparian litter and its residues (Cummins and Klug 1979). Intermediate-size streams have more scrapers in response to increased periphyton growth from greater light availability. In the extensively shaded, medium-size streams of the coastal redwood zone, however, community structure tends

Table 6.2. Influences of Timber Harvest on Physical Characteristics of Stream Environments, Potential Changes in Habitat Quality, and Resultant Consequences for Salmonid Growth and Survival.

<i>Forest practice</i>	<i>Potential change in physical stream environment</i>	<i>Potential change in quality of salmonid habitat</i>	<i>Potential consequences for salmonid growth and survival</i>
Timber harvest from streamside areas	Increased incident solar radiation	Increased stream temperature; higher light levels; increased autotrophic production	Reduced growth efficiency; increased susceptibility to disease; increased food production; changes in growth rate and age at smolting
	Decreased supply of large woody debris	Reduced cover; loss of pool habitat; reduced protection from peak flows; reduced storage of gravel and organic matter; loss of hydraulic complexity	Increased vulnerability to predation; lower winter survival; reduced carrying capacity; less spawning gravel; reduced food production; loss of species diversity
	Addition of logging slash (needles, bark, branches)	Short-term increase in dissolved oxygen demand; increased amount of fine particulate organic matter; increased cover	Reduced spawning success; short-term increase in food production; increased survival of juveniles
	Erosion of stream-banks	Loss of cover along edge of channel; increased stream width; reduced depth	Increased vulnerability to predation; increased carrying capacity for age-0 fish, but reduced carrying capacity for age-1 and older fish
Timber harvest from hillslopes; forest roads		Increased fine sediment in spawning gravels and food production areas	Reduced spawning success; reduced food supply
	Altered streamflow regime	Short-term increase in streamflows during summer	Short-term increase in survival
	Accelerated surface erosion and mass wasting	Increased severity of some peak flow events	Embryo mortality caused by bedload movement
	Increased fine sediment in stream gravels	Reduced spawning success; reduced food abundance; loss of winter hiding space	
		Increased supply of coarse sediment	Increased or decreased rearing capacity

<i>Forest practice</i>	<i>Potential change in physical stream environment</i>	<i>Potential change in quality of salmonid habitat</i>	<i>Potential consequences for salmonid growth and survival</i>
		Increased frequency of debris torrents; loss of instream cover in the torrent track; improved cover in some debris jams	Blockage to migrations; reduced survival in the torrent track; improved winter habitat in some torrent deposits
	Increased nutrient runoff	Elevated nutrient levels in streams	Increased food production
	Increased number of road crossings	Physical obstructions in stream channel; input of fine sediment from road surfaces	Restriction of upstream movement; reduced feeding efficiency
Scarification and slash burning (Preparation of soil for reforestation)	Increased nutrient runoff	Short-term elevation of nutrient levels of streams	Temporary increase in food production
	Inputs of fine inorganic and organic matter	Increased fine sediment in spawning gravels and food production areas; short-term increase in dissolved oxygen demand	Reduced spawning success

Source: From Hicks et al. (1991).

toward that found at the upper end of most forest stream continua. Farther downstream, collectors (filter feeders) predominate; these species use the fine particulate organics that upstream communities produce and fail to retain. The recycling of nutrients and ingestion of fine particulate matter from upstream areas is referred to as *nutrient spiraling* (Newbold et al. 1982; Mulholland 1992). Predators occur all along the continuum, eating each other and other consumers. Besides invertebrate predators, most aquatic and semiaquatic vertebrates are also predators (table 6.2, fig. 6.2), although some fish (e.g., California roach and Sacramento sucker) eat significant amounts of plant material (Moyle 1976). The carcasses of spawned-out anadromous fish, before they were depleted, were a major component of the nutrient cycle in stream ecosystems, providing inputs from the marine environment (Cederholm et al. 1989; Bilby et al. 1996). Assigning a species to a particular functional group or trophic level is not always possible because many species exhibit ontogenic shifts in feeding habits. For

example, many aquatic insects in early life-history stages are collectors, later becoming shredders or predators (Merritt and Cummins 1978).

An important, but little studied or understood component of the stream environment is the hyporheic zone, the area of flow below the streambed (fig. 6.3; Stanford and Ward 1988; Grimm and Fisher 1984; Triska et al. 1989a; Ward 1994; Duff and Triska 1990). This zone may extend vertically to depths of several meters and laterally from tens to hundreds of meters depending on channel confinement and floodplain geology (Stanford and Ward 1988). The stream bottom, although sometimes viewed as a boundary for the biological community, is the transition zone between the more rapidly flowing water of the active channel and the slower moving water of the hyporheic zone. In some streams, this subsurface flow can comprise 30-60 percent of the streamflow (Spence et al. 1996) and, in seasonally intermittent streams, all of the flow. Physical, chemical, and biological interactions within the hyporheic zone affect

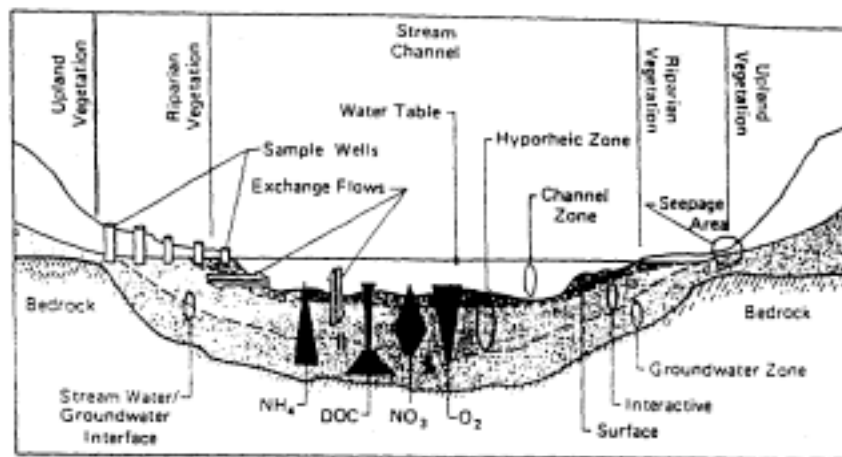


Figure 6.3. Conceptual model of the groundwater-surface water linkage at Little Lost Man Creek. Waters are divided into three zones: a channel zone containing surface water, a hyporheic zone, and a groundwater zone. The hyporheic zone has been divided into a surface hyporheos with virtually identical chemistry to channel waters, and containing > 98 percent advected channel water, and an interactive hyporheos characterized by physical-chemical gradients (e.g., NH_4 , O_2 , DOC, NO_3 , O_2 , temperature). The interactive zone consists of less than 98% but more than 10% advected channel water. The overall solute concentration is theoretically represented by the shape of the concentration profile. Transport of solutes across the groundwater-stream water interface (the stream boundary) is a function of the hydrologic head of the adjacent landscape or response to a concentration gradient, whereas transport from the channel zone to the hyporheic zone is dominated by advective processes. (From Triska et al. 1989b.)

nutrient cycling, dissolved oxygen, microbial processes, and stream temperature. A rich biological community lacking primary production by photosynthesis inhabits this subsurface habitat. Although dominated by meiofauna (bacteria, fungi, protozoans) and invertebrates, some vertebrates use the hyporheic zone for reproduction (e.g., lampreys, sculpins, and salmonids), shelter from high streamflows (e.g., salmonids and Pacific giant salamanders), or feeding (e.g., Pacific giant salamanders). Triska et al. (1989a) and Duff and Triska (1990) studied nitrogen dynamics and flow in the hyporheic zone of Little Lost Man Creek (tributary to Prairie Creek in Humboldt Co.), where approximately 92 percent of the streamside vegetation is old-growth redwoods. Dissolved oxygen levels in the hyporheic zone immediately adjacent to the stream were 100 percent saturated, but that saturation dropped to as low as 7 percent 11 m inland from the stream (fig. 6.3). Observed denitrification in the hyporheic zone demonstrated that microbial activity changed the water quality as it passed through the zone.

Stream Responses to Catchmentwide Processes

Riparian vegetation mediates the delivery and flow of material in stream channels, but in the redwood region stream conditions are also strongly controlled by dynamic, catchment-scale physical processes. A geologic terrain dominated by tectonically sheared and uplifted rocks overlain by unconsolidated sediments and locally deep colluvium, exposed to a climate of wet winters with periods of intense rainfall and runoff, produces a region known for some of the highest recorded rates of natural erosion and sediment transport (Janda et al. 1975; Kelsey 1980; Mattole Sensitive Watershed Group 1996). Large debris slides, extensive and deep-seated earthflows, and long-runout debris flows and debris-charged floods are frequent and widespread in the redwood region; their effects are often of sufficient magnitude and persistence that riparian vegetation along streams in the redwoods region, rather than resisting them, is modified and strongly shaped by them (Lisle 1989). This phenomenon is exemplified by the loss of old-growth redwood stands along Redwood Creek from channel expansion and accelerated lateral erosion caused by increased sediment loads from upstream and upslope sources (Janda et al. 1975). Even centuries-old redwood trees cannot resist the physical forces that are magnified by recent human alteration of erosion and sedimentation regimes in the catchment of Redwood National Park.

Upland or catchmentwide land use exacerbates naturally high erosion and sedimentation rates in many ways. Roads built to access timber alter flow and sediment patterns by extending drainage networks and providing direct connectivity of sediment delivery from eroding road surfaces to channels at stream crossings (Wemple and Jones 1996; Ziemer and Lisle 1998). Plugging or overflow of road culverts causes flow diversion and gully erosion, which deliver large

quantities of sediment to downstream channels (Hagans and Weaver 1987; Weaver et al. 1995). Removal of forest cover from steep or marginally stable hillslopes can trigger or accelerate mass failure through several mechanisms that affect soil water and root strength (Kelsey 1980; Sidle et al. 1985). The incidence or size of landslides typically increases in logged catchments, and some landslides propagate into debris floods or sediment-charged debris floods that reshape channel morphology and riparian vegetation for many kilometers downstream of the site of initiation (Kelsey 1980; Frissell et al. 1997; Pacific Watershed Associates 1998).

These changes in erosion and sediment regimes pose substantial and long-standing consequences for stream channels and floodplains, as well as their biota. Masses of deposited sediment can be flushed from steep tributary streams within years or decades (Madej 1987), but the delivery, residence, and transport of the sediment reconfigure and destabilize headwater stream habitats. The sediments are exported downstream to low-gradient reaches that were of greatest historical importance for production of salmon and other aquatic biota (Hagans and Weaver 1987; Frissell 1992; Frissell et al. 1997). Sediments generated as a result of natural or human disturbances in the landscape, once deposited in alluvial channels and floodplains, may have long residence times and thus influence channel conditions for many decades, in some cases probably more than a century (Madej 1987; Madej and Ozaki 1996). Alluvial stream channels in the redwood region and adjacent coastal regions respond by widening, shallowing, and losing pools and summer surface flow (Lisle 1982; Frissell 1992). Floodplain surfaces, channel beds, and large woody debris structures are destabilized (Lisle 1989; Madej and Ozaki 1996), leading to increased incidence of scour and fill of sufficient magnitude to kill the eggs and fry of salmon (Frissell et al. 1997), as well as other biota that seek refuge in bed interstices (Welsh and Ollivier 1998) or off-channel areas during high flows.

Comparative chronosequential studies of historical air photos, maps, and other documentary sources indicate that many streams in the redwood region, with their catchments extensively disturbed by logging, agriculture, roads, and other land uses, have experienced dramatic physical changes during the past three to seven decades, consistent with the described pattern of stream response to increased sediment loading (Madej 1987; Madej and Ozaki 1996). Partial physical recovery has been observed in many streams in the years following large storm events, but for many other streams, full recovery of natural sediment-transport regimes and channel morphology and behavior will likely take decades or centuries.

Few catchments in the redwood region have escaped extensive human disturbance and the accompanying transformation of fluvial dynamics over the past forty to one hundred years; most of the relatively pristine basins are small. These catchments should be considered landscape refugia, isolates where a sem-

blance of natural-historical erosion and sedimentation regimes remain locally intact, and which consequently are likely to be associated with high values for salmon and other aquatic biota that have declined precipitously elsewhere in the region (Frissell 1992; Frissell and Bayles 1996; Mattole Sensitive Watershed Group 1996).

The Role of Disturbance

The role of disturbance in structuring stream communities has been a primary focus of aquatic ecology for the past decade (Resh et al. 1988; Townsend 1989; Stanford and Ward 1992; Reeves et al. 1995; Spence et al. 1996; Wootton et al. 1996). Some changes are cyclic, such as seasonal variation in solar radiation, temperature, discharge, and leaf-fall. Less predictable but longer-lasting disturbance events, such as major floods, fires, mass-wasting events, and extreme winds that lead to windfall in the riparian zone, can influence the physical environment, and thus the biological community, for decades to centuries. Natural disturbances (i.e., floods, fires, mass wasting caused by previous events and earthquakes) and human activities (i.e., timber harvest, agriculture, mining, urban development, dams, and bank channelization) alike change the riparian communities associated with stream systems (Gregory et al. 1989; Schlosser 1991; Sedell et al. 1997; Frissell et al. 1997).

In the absence of human activities, based on the resistance-resilience model of ecosystem stability (Waide 1995), the late-seral redwood ecosystem is one of the most stable on the planet, achieving a self-perpetuating steady state (Bormann and Likens 1979), with a low incidence of severe fire (Veirs 1982). In such a stable ecosystem, disturbances tend to be localized within subdrainages (e.g., forest gap dynamics and landslides), their effects very limited in scope. Logging introduces a new disturbance regime. In coastal Oregon, the species diversity of salmonid fish assemblages was reduced in watersheds with more than 25 percent of the old-growth forest harvested (Reeves et al. 1995). Though large, natural disturbance events tend to be infrequent and cause large but localized changes to stream systems (pulse or stochastic events), human-caused changes are often more frequent and affect larger regions of the landscape (press or deterministic events) (Yount and Niemi 1990). In the redwood region, stream communities are shaped both by past natural disturbances and by a pervasive legacy of past and present human activities. Timber harvesting, as currently practiced in the region, represents an extreme disturbance to natural ecosystem processes—it is occurring on a scale and at a rate well beyond any natural disturbance the landscape has experienced in recent history (see Reeves et al. 1995; chap. 2, this volume). As indicated by the extensive loss of native biota, especially aquatic and riparian forms such as the many salmonid stocks in decline in northwestern California, the disturbance may already be irreparable for many species (Stouder et al. 1997).

The Aquatic Biota

In this section, we examine the aquatic and riparian life-forms of the redwood region and discuss their natural histories and roles in the ecosystem. We devote most attention to fish and amphibians, but also review briefly what is known about other taxa. (Appendix 6.1 lists plant and vertebrate species associated with aquatic ecosystems of the redwood region.)

Bacteria, Fungi, and Metazoans

The bacteria, fungi, and metazoans (protozoa, rotifers, copepods, nematodes, etc.) are extremely important but little-studied organisms of streams in the redwood region. These microscopic life-forms live in the hyporheic zone and the stream substrate, constituting part of the biofilm covering the streambed (Ward 1994). They fix dissolved organic carbon, break down detritus (fine and coarse particulate organic materials), and form a vital series of links in the aquatic food web (fig. 6.4) (Dahm 1981; Allan 1995).

The metazoans are microconsumers, which, in turn, are eaten by aquatic

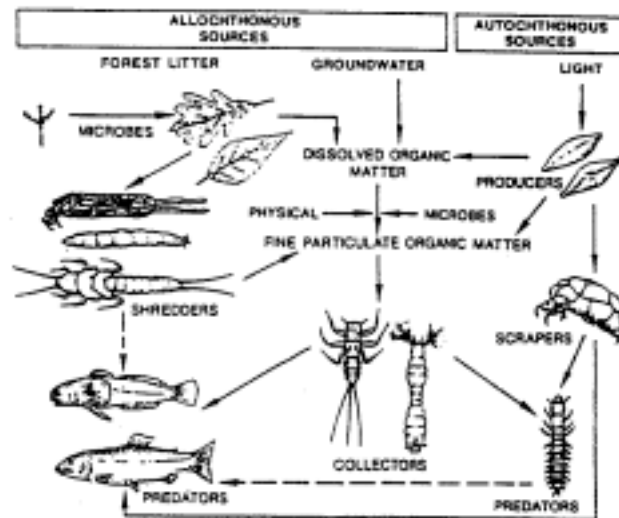


Figure 6.4. Energy sources for energy-flow pathways in, and the trophic structure of, woodland stream ecosystems. Deciduous leaves, photosynthesis by diatoms, and dissolved organic matter in groundwater are major energy sources. Genera that typify consumer functional groups are the shredders *Pteronacys* (above), *Tipula*, and *Pycnopsyche*; the collectors *Stenonema* (middle) and *Simulium*; the scraper *Glossoma*; and the predators *Nigronia* (lower right), *Cottus*, and *Salmo* (left). Litter microbes are characterized by hyphomycetes fungi. The dashed arrow indicates infrequent exchange. Organisms are not drawn to scale. (From Murphy and Meehan 1991 as adapted from Cummins 1974)

insects and other macroconsumers. The hypomycete fungi, which break down leaves and other riparian litter, are important energy sources for the shredders, which convert coarse particulate material to fine particulate material (fig. 6.4). The studies by Triska et al. (1989a,b) and Duff and Triska (1990) are among the few published accounts of bacterial activities in streams of the redwood region. Triska et al. (1989b) state that "further understanding of hyporheic metabolism and nutrient dynamics is required if we are to holistically address the biological continuum of river networks." We are not aware of any studies involving production or food web dynamics of bacteria, fungi, or metazoans in aquatic habitats of the redwood region.

Plants

Algae, mosses, and vascular plants constitute the aquatic primary producers in streams, providing autochthonous organic material. These plants require dissolved nutrients and a suitable substrate to fix solar energy. Iwatsubo et al. (1975, 1976) provided species lists of plants identified in Redwood National Park and reported that the periphyton community (food source for scrapers or grazers) is dominated by the diatoms *Achnanthes lanceolata*, *Diatoma vulgate*, *Gomphonema angustatum*, and *Aelosira varians*. Power (1991, 1992) studied algal dynamics (*Chidophora glomerata*) in the South Fork Eel River on the eastern edge of the central redwood section. Mosses, which are major primary producers in headwater streams, and vascular plants (e.g., *Potamogeton* and *Rupia*) are locally abundant in larger streams and estuaries but are little studied in the redwood region and clearly warrant more research.

Macroinvertebrates

Iwatsubo et al. (1976), Iwatsubo and Averett (1981), and Harrington (1983) provided species lists of macroinvertebrates in Redwood National Park. Harrington (1983) found seven orders of aquatic insects, including mayflies, stoneflies, caddisflies, beetles, dragonflies and damselflies, and true flies. No endemic aquatic macroinvertebrates have yet been described for the redwood region, but this may be due to a lack of systematic research efforts. Much more research is warranted on these important aquatic species, particularly interdisciplinary studies that include chemical, physical, and biological interactions.

Fish

Compared with other regions of North America, the Pacific Coast has low species diversity of fish (Moyle 1976; Moyle and Herbold 1987; Reeves et al. 1998). The redwood region includes portions of two of the six native fish provinces within California (the Klamath and the Sacramento--San Joaquin) (Moyle 1976), but none of the endemic species of these two provinces is confined to the redwood region. The redwood region supports a few endemic ter-

restrial vertebrates (chap. 5), but no endemic fish or other aquatic vertebrates. Most of the fish species native to the redwood region are anadromous (e.g., salmon, sturgeon, and lampreys), euryhaline (able to move between marine and fresh waters, e.g., sticklebacks and sculpins), or are descended from marine ancestry (e.g., three species of stream-dwelling sculpins). The only naturally occurring (nonintroduced) representatives of truly freshwater fish species (those not capable of colonizing via the marine environment) in the redwood region are two sucker and five minnow species (table 6.3), all derived from the Sacramento-San Joaquin River system (Moyle 1976).

Moyle (1976) describes three fish zones in streams within the California coastal region: (1) a resident trout zone (rainbow trout in streams south of the Eel River and either rainbow or cutthroat trout in streams from the Eel River north) located in upper stream sections above barriers to anadromous fish; (2) an anadromous fish zone (lampreys, salmonids, sculpins, suckers, and minnows); and (3) an intertidal zone (euryhaline species listed in table 6.3) or estuary that may extend inland from the ocean for several kilometers (e.g., Navarro, Eel, Mad, Klamath, and Smith Rivers), or much less than a km ending at the first rocky riffle (e.g., Wilson and Mill Creeks in Humboldt Co.). The presence or absence of Fish is a primary determinant in classifying streams under the California Forest Practice Act (discussed later in this chapter and in chap. 8).

Anadromous salmonids in the redwood region (i.e., Chinook and coho salmon, and rainbow [steelhead] and cutthroat trout) have somewhat similar life-history patterns and habitat requirements; each has been considered for listing under the Endangered Species Act (ESA) (NMFS 1998). These four species coexist in some streams by spawning and rearing in different areas or at different times. Chinook salmon typically spawn lower in a basin than coho salmon, with steelhead and cutthroat trout spawning progressively farther upstream. Juvenile salmonids (known by several names, including fry, fingerlings, parr, yearlings, young-of-year [YOY], etc.) grow in streams for several months to several years, depending on intrinsic (genetic makeup) and environmental conditions. At the end of their stream-rearing stage, the juveniles undergo a physiological change, the parr-smolt transformation, which adapts them for marine conditions.

Chinook salmon, the largest of the Pacific salmon, once populated large coastal streams as far south as the Ventura River (Moyle 1976). Their present range in coastal streams extends south only to the Mattole River in Humboldt County (G. Bryant, pers. comm.). Four different Chinook runs or life-history patterns occur in California (Yoshiyama et al. 1998), the late-fall and winter runs occurring only in the Central Valley and the latter listed as endangered under the ESA. Only fall Chinook both spawn and rear in the redwood region. Spring Chinook salmon of the Klamath River system migrate inland of the redwood zone to spawn in the Salmon and Trinity Rivers. The Southern Oregon/

Table 6.3. Consumer Functional Groups of Stream Animals.

<i>Functional Group</i>	<i>Subdivision Based on Feeding Mechanisms or Dominant Food</i>	<i>Known Redwood Region Organisms</i>
Shredders	Detritivores: decaying vascular plant tissue	Trichoptera (<i>Hydatophylax</i> , <i>Lepidostomatidae</i>) Plecoptera (<i>Peltoperlidae</i> , <i>Pteronarcidae</i>) Diptera (<i>Holorusia</i>)
	Herbivores: living vascular plant tissue	Trichoptera (<i>Phryganea</i> , <i>Leptocerus</i>) Lepidoptera (<i>Pyrilidae</i>) Coleoptera (<i>Chrysomelidae</i>) Diptera (<i>Polypedilum</i> , <i>Lemnaphila</i>)
Scrapers	Rock substrate	Ephemeroptera (<i>Heptageniidae</i> , <i>Baetidae</i> , <i>Ephemerellidae</i>) Trichoptera (<i>Glossosomatidae</i> , <i>Neophylax</i>) Lepidoptera (<i>Parargyractis</i>) Coleoptera (<i>Psephenidae</i>) Diptera (<i>Thaumaleidae</i> , <i>Deutera-phlebiidae</i>)
	Wood substrate	Ephemeroptera (<i>Caenidae</i> , <i>Leptophlebiidae</i>) Trichoptera (<i>Heteroplectron</i>) Snails (<i>Juga</i>)
Collectors	Filter feeders	Ephemeroptera (<i>Isonychia</i>) Trichoptera (<i>Hydropsychidae</i> , <i>Brachycentridae</i>) Diptera (<i>Simuliidae</i> , <i>Rheotanytarsus</i> , <i>Culicidae</i>)
	Deposit feeders	Ephemeroptera (<i>Ephemeridae</i> , <i>Baetis</i> , <i>Paraleptophlebia</i>) Diptera (<i>Chironomini</i> , <i>Psychodidae</i>)
Predators	Swallowers of whole animals	Odonata Plecoptera (<i>Perlidae</i>) Megaloptera Trichoptera (<i>Rhyacophilidae</i>) Coleoptera (<i>Amphizoidae</i>) Diptera (<i>Tanypodinae</i> , <i>Empididae</i>) Fish (<i>Salmonids</i>) Amphibians (frogs, toads, salamanders) Reptiles (lizards, snakes, rudes) Birds (kingfishers, mergansers) Mammals (otters, bears)
	Piercers of tissue fluids	Hemiptera (<i>Belastomatidae</i> , <i>Notonectidae</i>) Coleoptera (<i>Dytiscidae</i>) Diptera (<i>Tabanidae</i>)

Source: Modified from Cummins (1973); Merritt and Cummins (1978).

Northern California Chinook salmon Evolutionarily Significant Unit (ESU) was proposed for listing as threatened in March 1998 (NMFS 1998).

Fall Chinook salmon in coastal California typically return to their natal streams during early fall after two to four years in the ocean and spawn between November and February. Female salmon construct their nests (redds) in the stream substrate of mainstem rivers and larger tributaries, where the eggs are buried after fertilization by males. Egg numbers can range from 2,000 to 14,000, depending on the size of the female (Moyle 1976). Fry emerge from the gravel in spring and begin feeding on drifting aquatic and terrestrial insects. They usually complete their stream growth and migrate to the ocean within three to six months at a total length of 70-90 mm (Healey 1991).

Coho salmon historically may have occurred as far south as the Big Sur River, but the southernmost naturally spawning populations now are in Scott and Waddell Creeks (Brown et al. 1994). All coho salmon populations in the coastal redwood region currently are listed as threatened (NMFS 1998). The life history of coho salmon in California was detailed in a classic study carried out primarily on Waddell Creek by Shapovalov and Taft (1954). Sandercock (1991) provided a detailed review of coho salmon biology throughout the range of the species. Unlike Chinook salmon, with several genetically distinct life history patterns, all coho salmon populations in California have similar life cycles. They typically spend fifteen to eighteen months in streams before smolting and entering the ocean. Most adult coho return to natal streams about eighteen months later, at age three, for spawning in late fall or early winter. Coho generally spawn in smaller streams than Chinook salmon, but in some streams (e.g., Prairie Creek) both species may spawn in the same area, Chinooks spawning earlier than coho. Female coho usually construct redds at the outlet of a pool (upstream end of a riffle) in small- to medium-size gravel. Depending on the size of the female, 1,000 to 5,000 eggs are deposited in the redd (Moyle 1976).

Coho salmon fry emerge from the gravel in early spring, move to the stream margins, and begin feeding on small invertebrates. As they grow they move into progressively deeper water, favoring pools with wood, shade, and other forms of cover. juveniles feed primarily on aquatic invertebrates, but terrestrial prey (e.g., ants, beetles, spiders) may predominate in late summer to early fall (Sandercock 1991). In late fall to early winter, juvenile coho move into alcoves or side channels along the stream channel or congregate in deeper pools with wood to overwinter during times of high flows. Smolting and migration to the ocean typically take place in March through May, when the fish are 10-14 cm in total length.

Steelhead trout (anadromous rainbow trout) currently occur along the California coast as far south as Malibu Creek (NMFS 1998), well south of the redwood zone and the southernmost distribution of any anadromous salmonid. The three southernmost ESU populations of steelhead are currently listed as

endangered (Southern California ESU) or threatened (South-central California Coast, and Central California Coast ESUs) (NMFS 1998). National Marine Fisheries Service (NMFS) (1998) determined that listing was not presently warranted either for the Northern California ESU or the Klamath Mountain Province ESU.

Steelhead in California exhibit one of two life histories, either summer-run or winter-run. These run types are based on the timing and state of gonadal development when adult steelhead reenter freshwater from the ocean and location and timing of spawning (reviewed by Roelofs 1983). Steelhead in the redwood region are winter-run populations, except for a small run of summer steelhead in Redwood Creek, typically fewer than fifty fish annually (David Anderson, pers. comm). Summer steelhead migrate upstream beyond the redwood zone in the Eel, Mad, and Klamath Rivers (Roelofs 1983).

Shapovalov and Taft (1954) noted that "unlike silver (coho) salmon, steelhead migrate to sea at various ages and over a long period within a season, spend varying amounts of time in the ocean, are capable of spawning more than once, sometimes spawn before their first journey to the sea, and may even remain in fresh water for their entire lives." Adult winter-run steelhead return to spawn in coastal streams beginning in late fall and continuing through winter and early spring (April). There may be some overlap in spawning areas used by coho salmon, but steelhead usually migrate farther upstream to construct redds and deposit eggs. The number of eggs produced ranges from around 1,000 to more than 10,000, depending on female size (Shapovalov and Taft 1954). Fry emerge in late spring through early summer and begin feeding on small invertebrates at the stream margin. Individual fry that survive and grow move into deeper, faster water, where they continue feeding on drifting prey.

The most common life-history pattern for coastal steelhead populations south of Alaska is two years of freshwater rearing and returning to spawn after two years in the ocean (Busby et al. 1994). In Waddell Creek between 1933 and 1941, 56 percent of the steelhead returning to spawn had reared one year in the ocean; 44 percent had spent two years (Shapovalov and Tale 1954). Adult steelhead can survive spawning, return to the ocean, and spawn a second or third time (Busby et al. 1994). In a sample of 3,888 adult steelhead, Shapovalov and Taft (1954) found that 83 percent were on their first spawning run, 15 percent on their second, and 2 percent on their third. Steelhead that survive to spawn a second or third time are most likely to be females (Busby et al. 1954).

Coastal cutthroat trout in the redwood region occur south to the Eel River and range inland 8-48 km, with the Smith River having the most substantial populations (Gerstung 1997). All coastal cutthroat trout populations in California, Oregon, and Washington are currently being evaluated for listing under the ESA (NMFS 1998) and are classified as a Species of Special Concern by the California Department of Fish and Game (Gerstung 1997). The life his-

tory of coastal cutthroat trout is complicated and poorly documented. Populations can be resident (existing upstream of migration barriers to other migratory fish), potamodromous (spawning in small tributaries but residing in larger streams as adults), or anadromous, although anadromy is "sporadic or uncertain in California populations" because adult fish may remain in estuaries instead of entering the ocean (Gerstung 1997).

Coastal cutthroat spawn during winter and early spring in small tributaries upstream of areas used by steelhead trout if accessible (Gerstung 1997). Fry emerge at a size of about 25 mm and move to the stream margins to feed on small invertebrates, primarily insects (Trotter 1997). When sympatric, juvenile cutthroat trout utilize stream habitats and food resources similar to those of juvenile coho and steelhead and may be limited by competitive interactions (Trotter 1997). Mitchell (1988) found that sympatric populations of steelhead and cutthroat greater than 10 cm long partitioned stream habitat by selective segregation, cutthroat rearing in deeper, slower water, steelhead in shallower, swifter water of runs, rapids, and the heads of pools. Age one and older cutthroat trout are opportunistic predators that feed on invertebrates and fish, including other salmonids (Trotter 1997). Most anadromous cutthroat trout smolt at ages two, three, or four, but can be as young as one or as old as six (Trotter 1997). Like steelhead, coastal cutthroat trout can spawn repeatedly in successive years, with up to five times reported (Trotter 1997).

Other fish in table 6.3 mentioned by Moyle et al. (1995) as species of special concern include green sturgeon, eulachon, longfin smelt, and tidewater goby (now listed as federally threatened). These authors also note that Pacific lamprey numbers are declining in California.

Herpetofauna

Streams, ponds, lakes, and associated riparian habitats of the coastal redwood forests of northern California are relatively rich in herpetofauna (amphibians and reptiles), supporting up to eighteen species of amphibians (one toad, four frogs, and thirteen salamanders) and eleven species of reptiles (four lizards, six snakes, and a turtle) (Stebbins, 1985). With two exceptions—western pond turtle and Oregon aquatic garter snake—these reptiles are not aquatic but may frequent the riparian zone, where they often forage on the abundant invertebrates at the water's edge. The nonaquatic reptiles (western fence lizard, western skink, northern and southern alligator lizards, rubber boa, ringneck snake, sharptail snake, and the western terrestrial, northwestern, and common garter snakes) are discussed in chapter 5.

The seven terrestrial, direct-developing salamanders of the family Plethodontidae are discussed in chapter 5. The other ten amphibians of the redwood region can be placed into one of two main groups based on their reproductive behavior—those species that breed primarily in lentic habitats (ponds

and lakes) and those that breed primarily in lotic (stream) habitats. Some of these species, however, will breed in both types of aquatic habitat. The species most closely associated with lentic habitats are the northwestern salamander, rough-skinned newt, Pacific tree frog, red-legged frog, and the western toad (Stebbins 1985). The rough-skinned newt, red-legged frog, and western toad also breed in slow-moving streams. Those species most closely associated with streams for breeding are the giant salamanders, with two species in the redwoods, the Pacific giant salamander and the California giant salamander (Good 1989), the southern torrent salamander (Good and Wake 1992), the red-bellied newt, the tailed frog, and the foothill yellow-legged frog (Stebbins 1985).

Pond- and lake-breeding species show site fidelity from generation to generation, with most individuals returning to the same body of water to reproduce (e.g., Semlitsch et al. 1996). Adult red-legged frogs, northwestern salamanders, and Pacific tree frogs usually migrate from upland foraging and resting habitats to breeding sites in late winter or early spring (Stebbins 1985). The rough-skinned newt migrates in early to late spring and the western toad from late spring to early summer (Stebbins 1985). These migration events are not absolutely fixed in time but are triggered by changes in climatic conditions in the vicinity of breeding sites in the appropriate season (e.g., Packer 1960; Semlitsch et al. 1993; H. Welsh, unpub. data).

Adult red-legged frogs, northwestern salamanders, and rough-skinned newts—all forest-dwellers—migrate to slow-moving streams, ponds, or lakes to seek mates, amplex, and deposit eggs. The western toad and the Pacific tree frog are the least specialized, occurring across a wide range of habitat types, from forest to meadow, and breeding in a variety of standing waters. Western toads select larger bodies of water than tree frogs and often take advantage of side pools along rivers, such as the Eel and the Trinity, during the waning flows of late spring. Thousands of newly metamorphosed toadlets are often encountered along riverbanks adjacent to these backwaters in late summer. Pacific tree frogs will breed in cattle tanks, wallows, roadside ditches, and large puddles, as well as in larger bodies of standing water (Stebbins 1985).

Lotic or stream-breeding amphibians make up a major component of the biomass in streams throughout the Pacific Northwest and can exceed fish in numbers and total biomass (e.g., Hawkins et al. 1983). Recent studies in the redwoods indicate that stream habitats in these forests support large numbers of amphibians (Welsh et al. 1997; Welsh and Ollivier 1998). Amphibians that breed in lotic habitats often show considerable specialization in their use of such waters. For example, the southern torrent salamander is a headwater specialist, breeding in springheads and other emergent water sources (Nussbaum 1969). It requires cold, clear, shallow water flowing over clean, coarse streambed substrates (Welsh and Lind 1996). In the interior parts of its range in California, it is closely associated with late-seral forests (Welsh 1990).

Pack giant salamanders breed in streams from headwaters along the length of the stream continuum to larger streams and rivers. Females lay 75 to 100 eggs under large streambed substrates, primarily in riffles, and usually guard the nest until the eggs hatch. The aquatic larvae typically take two to three years to mature and metamorphose to a terrestrial form (Leonard et al. 1993). This salamander has evolved a dual life-history strategy, in which some individuals forego metamorphosis. These animals instead become sexually mature while retaining larval traits, including gills, which allow them to remain in the stream (becoming paedomorphs). They are voracious stream predators, feeding on anything they can swallow, including fish, invertebrates, and other giant salamanders (Parker 1994). The terrestrial phase of the giant salamander is also a voracious predator, taking small mammals and snakes as prey (Leonard et al. 1993). Welsh captured a large adult that regurgitated an adult chaparral mouse. Giant salamanders will also eat a wide range of invertebrate prey, including banana slugs.

The tailed frog breeds in headwaters to somewhat larger streams (e.g., Karraker and Beyersdorf 1997), occurring in highest abundances upstream of waters occupied by anadromous fishes. Larval tailed frogs require streams with cold, clear waters and clean, coarse substrates (Welsh 1993; Welsh and Ollivier 1998; Welsh and Lind in review.). Adults are found in the riparian zone near streams, where they forage at night along the stream banks. Adult tailed frogs are highly philopatric (Daugherty and Sheldon 1982a) and long-lived (Daugherty and Sheldon 1982b).

The foothill yellow-legged frog occurs farther down the stream continuum than the tailed frog or torrent salamander, preferring more open areas along larger streams and rivers where it often can be observed sunning on rocks and gravel bars. This species breeds in the slower-moving portions of these streams and rivers, attaching its eggs to rocky substrates in shallow, slow-flowing water near the stream margins (Zweifel 1955; Fuller and Lind 1992; Kupferberg 1996; Lind and Welsh, unpub. data).

The red-bellied newt is perhaps the closest to an endemic vertebrate in the redwood forest (see Twitty 1964 and chap. 5, this volume). Although it is biogeographically restricted to northwestern California within the range of coast redwood, it is not found exclusively in redwood forest habitats. It also occurs in mixed Douglas-fir-hardwood forests and adjacent meadowlands (Stebbins 1985; H. Welsh, personal observations). Red-bellied newts are active on the forest floor, mainly at night and only when litter moisture is high, throughout all but the summer months (H. Welsh, unpub. data). They migrate to breeding sites as early as the first week in February (Stebbins 1985; H. Welsh, unpub. data).

The western pond turtle is the only freshwater turtle in the redwood region. This turtle is found along large bodies of water, including lakes, ponds, and streams. It is spotty in occurrence, associated with areas having secure basking

sites (e.g., logs and rocks surrounded by water) and undercut banks, where turtles can seek cover to avoid such predators as river otters, raccoons, and minks (Reese and Welsh 1998). It is a long-lived species and can reach fairly high densities where conditions are favorable. Pond turtles use upland forest habitats both for nesting and overwintering (Reese and Welsh 1997). On the whole, this species is uncommon in most areas of the redwoods, but populations do occur along parts of the major rivers of the northern California coast. The Mattole River has pond turtles in relatively low numbers.

The Oregon aquatic garter snake is a highly aquatic snake found along both small and large streams, ponds, lakes, and marshes, where individuals forage primarily on amphibians and fishes. At Hurdygurdy Creek in Del Norte County, juvenile snakes fed along stream margins on young-of-the-year steelhead and Chinook salmon or, when they become abundant in the summer, on tadpoles of the foothill yellow-legged frog (Lind and Welsh 1994). As adults these snakes shift prey preferences to larval and paedomorphic Pacific giant salamanders, which they pursue in the streambed substrates of even the fastest waters (Lind and Welsh 1990, 1994).

Birds

Bird species that depend on riparian/aquatic habitats in the redwood region are similar to those of riparian zones throughout northern California (e.g., osprey, bald eagle, belted kingfisher, American dipper, great blue heron, green heron, common merganser, killdeer, and spotted sandpiper). Most of these species are fish predators and therefore are positioned energetically at the top of the aquatic food web (e.g., fig. 6.5). Sustaining viable populations of these top predators

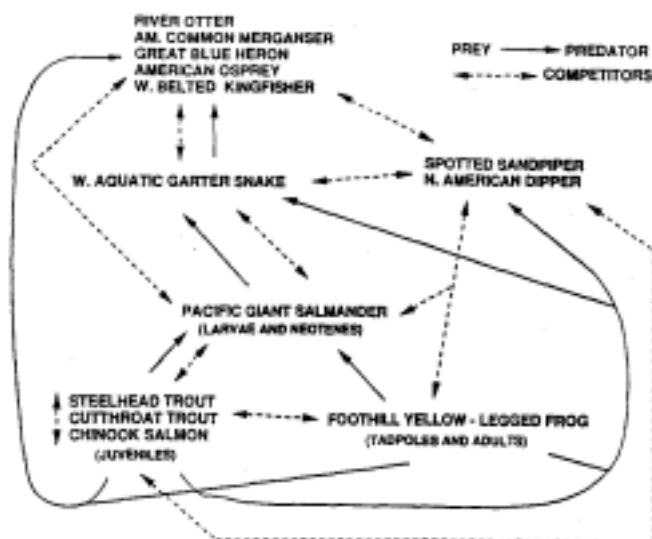


Figure 6.5. Vertebrate food web relationships at Hurdygurdy Creek, Del Norte County, California. (From Lind and Welsh 1990, 1994, unpub. data, and personal observations. Drawing by A. Lind.)

requires a healthy, productive riparian/aquatic ecosystem, a condition that is increasingly rare in the redwood region because of negative impacts from timber harvesting, water diversions, agricultural runoff, and introduced exotic predators. Many other birds species occur periodically or marginally in the riparian zone; these are addressed in chapter 5.

Mammals

Mammal species that utilize the riparian/aquatic habitats of the redwood region (e.g., river otter, mink, muskrat, raccoon, black bear) are similar to those found in riparian zones throughout northern California and southwestern Oregon. Most of these mammals eat fish or other aquatic vertebrates, as well as invertebrates, such as crayfish. Like the birds just mentioned, these species are positioned energetically high on the food chain (fig. 6.5); thus, sustaining their populations similarly requires productive, healthy aquatic ecosystems. Bats depend on open aquatic habitats for water (drinking on the wing) and aerial feeding (eating insects, many of which have aquatic larvae, and other flying arthropods). Proximity of aquatic and riparian areas to roost sites is essential for bats of the redwood region, species which include California myotis, little brown bat, long-legged bat, long-eared bat, Yuma myotis, hoary bat, and silver-haired bat (McKenzie et al. 1994).

Changes in Stream Ecosystem Processes Resulting from Timber Harvesting and Related Activities

The spatial and temporal scales of continuous timber harvest within the redwood region have led to widespread and persistent changes in stream conditions (table 6.4). The most pronounced change is the absence of, or reduction in, large trees within and adjacent to stream channels. Napolitano (1998) compared present-day log volumes in a historically (1864-1904) clear-cut and splash-dam logged, second-growth coastal redwood stream (north fork of Caspar Creek) (24 kg/m^2) with nine similar streams in old-growth redwood ($49\text{-}268 \text{ kg m}^2$). (See Gates [1983] for a description of the highly destructive practice of splash-dam log transportation.) The pronounced difference in the abundance of large logs between Caspar Creek and the old-growth streams resulted in lasting channel changes, including channel incision, simplification of form, and reduction in sediment storage capability. Summarizing thirty years of research on the effects of timber harvesting on Caspar Creek, a 2,162-ha redwood-dominated watershed in the Jackson State Forest of Mendocino County, Ziemer (1998a) noted that logging had increased summer low flow (Keppeler 1998), subsurface and soil pipe flow (Keppeler and Brown 1998), and riparian tree mortality due to blow-down (Reid and Hilton 1998), and modified other riparian conditions.

For potential long-term effects on aquatic biota and their habitats, one of the

Table 6.4. Stream-Dwelling Fish Species in the Redwood Biome.

<i>Anadromous</i>	<i>Euryhaline^a</i>	<i>Freshwater</i>
Pacific lamprey N (<i>Lampetra tridentata</i>)	prickly sculpin N (<i>Cottus asper</i>)	California roach N (<i>Hesperoleucus symmetricus</i>)
River lamprey N (<i>Lampetra ayresi</i>)	Coastrange sculpin N (<i>Cottus aleuticus</i>)	Speckled dace N (<i>Rhinichthys osculus</i>)
Pacific brook lamprey N (<i>Lampetra pacifica</i>)	Riffle sculpin N (<i>Cottus gulosus</i>)	Sacramento squawfish N (<i>Ptychocheilus grandis</i>)
Green sturgeon N (<i>Acipenser medirostris</i>)	Sharpnose sculpin N (<i>Clinocottus acuticeps</i>)	Hardhead N (<i>Mylopharodon conocephalus</i>)
White sturgeon N (<i>Acipenser transmontanus</i>)	Staghorn sculpin N (<i>Leptocottus armatus</i>)	Hitch N (<i>Lavinia exilicauda</i>)
Coho salmon N (<i>Oncorhynchus kisutch</i>)	Longfin smelt N, E (<i>Spirinchus thaleichthys</i>)	Tench I (<i>Tinca tinca</i>)
Chinook salmon N (<i>Oncorhynchus tshawytscha</i>)	Penpoint gunnel N (<i>Apodichthys flavidus</i>)	Golden shiner I (<i>Notemigonus crysoleucas</i>)
Pink salmon N, O (<i>Oncorhynchus gorbuscha</i>)	Saddleback gunnel N (<i>Pholis ornata</i>)	Carp I (<i>Cyprinus carpio</i>)
Chum salmon N (<i>Oncorhynchus keta</i>)	Tidewater goby N, E (<i>Eucyclogobius newberryi</i>)	Klamath smallscale sucker N (<i>Catostomus rimiculus</i>)
Sockeye salmon N, O (<i>Oncorhynchus nerka</i>)	Starry flounder N (<i>Platichthys stellatus</i>)	Sacramento sucker N (<i>Catostomus occidentalis</i>)
Rainbow trout N (<i>Oncorhynchus mykiss</i>)	Shiner perch N, E (<i>Cymatogaster aggregata</i>)	Brown bullhead I (<i>Ictalurus nebulosus</i>)
Cutthroat trout N (<i>Oncorhynchus clarki</i>)	Bay pipefish N, E (<i>Syngnathus leptorhynchus</i>)	
Eulachon N (<i>Thaleichthys pacificus</i>)	Threespine stickleback ^b N2 (<i>Gasterosteus aculeatus</i>)	
striped bass I (<i>Morone saxatilis</i>)		
American shad I (<i>Alosa sapidissima</i>)		

^a Lower estuarine zones may include several species of marine fish

^b Sticklebacks can be resident or anadromous

N = native; I = introduced; E = estuarine; O = occasional.

Source: Moyle (1976); McGinnis (1984); Dill and Cordone (1997).

most significant modifications of riparian conditions from logging evidenced in the Caspar Creek watershed was the alteration of the large woody debris regime (Lisle and Napolitano 1998). The initial increase of large woody debris from blow-down in the riparian buffers increased habitat heterogeneity by storing sediments and forming pools (Nakamoto 1998). Nevertheless, the limited size spectrum and species composition of this large woody debris, as a consequence of logging in the nineteenth century (Napolitano 1998), suggested that the

long-term result would be less favorable habitat conditions overall for aquatic species. Habitat suitability is expected to decline because the small, now hardwood-dominated woody debris decays quickly-much faster than that from conifers-and as input rates from depleted riparian sources in adjacent clear-cuts and buffer zones decline (Lisle and Napolitano 1998; see also Reid and Hilton 1998).

Riparian forests on heavily logged landscapes are often dominated by deciduous trees (i.e., alders, big-leaf maple, and willows), with a lesser component of second- or third-growth conifers. Red alder often dominates the riparian zones of coastal streams in clear-cut watersheds (Dahm 1981). Lacking large and well-distributed, rot-resistant conifer wood, and with excess sediment filling the streambed, many streams in the redwood region have fewer and shallower pools and a less diverse array of physical conditions than reference streams in pristine settings.

The physical habitat conditions in streams constitute the ecological context for organisms that evolved there (Holt and Gaines 1992; Southwood 1977). Stream communities in logged versus unlogged streams are often different because the former have unsuitable habitat for many aquatic organisms. For example, many small, non-fish-bearing streams logged during the past 40 to 100 years, which are largely unprotected by current forest practice rules, are covered by 1-5 m of debris and sediments (Welsh, pers. obs.). These buried stream channels frequently flow subsurface for tens of meters, providing little or no habitat for many native aquatic organisms. Lewis (1998) found that although changes in forest practice rules between the 1970s and the 1990s reduced the amount of suspended sediment in Caspar Creek, logged areas still accounted for 89 percent more sediment than unlogged areas. Much of this sediment appeared to be mobilized from the unbuffered first-order watercourses (Lewis 1998).

Stream Classification and Its Problems

Stream ecosystems are supposed to be protected by regulations regarding timber harvest. The greatest scientific shortcoming in the current California Forest Practices Act (see chap. 8), from the perspective of riparian and aquatic resources, is its reliance on the conceptual approach to stream buffer protections used in the California Department of Forestry (CDF) stream classification system. CDF uses a system of stream categories in which class I represents fish-bearing streams, class II represents streams supporting aquatic life other than fish, and class III represents streams not supporting aquatic life. This system is in contrast to the geomorphological system based on watershed position (Strahler 1957), where first-order streams receive the highest classification--headwater tributaries, which combine to create second-order streams, which then combine to make third-order streams, and so on. The CDF system fails to recognize that a stream ecosystem and its vital processes are a functional contin-

uum (fig. 6.2). The CDF system establishes differential protection measures along the stream continuum based on two factors, permanence of surface water and the presence of fish and other aquatic life. The presence of surface water has become the functional equivalent for the presence of aquatic life. Because headwater areas may have ephemeral surface flow (but perennial subsurface flow) and are not fish-bearing, they receive the least protection in terms of buffer zone width and retention of canopy cover and large woody debris. Perennial fish-bearing streams or rivers, under the CDF system, have the highest standards for these parameters.

Current buffer width designations have little basis in science. Rather, the different buffer widths for different stream classes reflect a bias in human valuation for game fishes over other riparian and aquatic biota, as well as ignorance of the stream continuum and the requirements of a healthy stream ecosystem upon which fish and other organisms depend. If relevant scientific data were considered, wider buffers would be provided on headwaters (CDF Class II and III or first- through third-order streams [Strahler 1957]) because they (1) tend to be transport reaches that provide crucial structural components such as LWD, (2) contribute a mixture of sorted coarse sediments of varying sizes downstream, and (3) are generally the source of the coldest waters. These headwater channels, if disturbed, are also potentially the greatest source of fine sediments, which can congest streambed interstices. Sediment-free interstices downstream are required for successful spawning by salmonid fishes; they also shelter the early life stages of stream macroinvertebrates and several species of stream amphibians (Welsh and Ollivier 1998). Consequently, headwater channels require significant riparian buffers to filter out fine-sediment runoff from the generally steeper terrain in which these channels are typically embedded.

The headwaters are where some of the stream biota thrive in the absence of fish predators. Some species appear to require areas with little or no predation in order to maintain viable populations on the landscape (e.g., see torrent salamander section below). Among such life-forms are several amphibians that require both aquatic and terrestrial environments in which to carry out their complex biphasic (aquatic and terrestrial) life histories. Among their terrestrial needs are cool, moist, stable microclimates in riparian forests alongside streams, where the adult life stages hide, forage, and seek mates. As currently constituted, even buffered areas along CDF Class I (fish-bearing) streams are primarily "edge" habitat (Laurance and Yensen 1990) and lack sufficient "interior core" areas where terrestrial microclimates are ameliorated and stabilized (Yahner 1988; Saunders et al. 1991; Brosnokske et al. 1997). Recent research suggests that no-harvest buffers of 30--60 m are required to maintain suitable streamside and aquatic conditions for several cold-temperate adapted amphibian species (Brosnokske et al. 1997; Ledwith 1996; Welsh and Hodgson, unpub. data).

The majority of large woody debris in a healthy stream enters the system

in the headwaters and upper tributaries of the stream network, with less contributed along the larger, lower stream reaches (Maser et al. 1988). Adequate provisions for this ecosystem component are absent from the California Forest Practices Act for Class III, and insufficient for Class II streams. No leave trees (retained trees) are required or designated (dedicated) in the riparian management zone (RMZ) that might eventually contribute large woody debris greater than 61 cm to the Class II stream networks. Under current rules, the largest trees can (and probably will) be removed from the RMZ. Without provisions in the rules for some number of well-distributed, dedicated trees for recruitment of large woody debris, especially in size class 5 (>61 cm dbh; Mayer and Laudenslayer 1988), along the entire stream continuum, this critical structural element (table 6.1; Sedell et al. 1988) will continue to be lacking from the upper reaches of the stream networks of the redwood landscape.

By ignoring these considerations, the CDF system establishes and maintains a negative feedback system whereby downstream habitats can be progressively and continuously degraded because the headwaters are unprotected. The Mattole River Basin, and many other severely degraded watersheds on the North Coast, reflect this process of serial magnification of negative cumulative effects from poor timber-harvest practices (Mattole Sensitive Watershed Group 1996; MRC 1989). The result is a cascading disaster for aquatic and riparian resources where even portions of the stream that may initially support fish (CDF Class I or third-order and higher stream reaches) shrink and retreat with each harvest re-entry in a drainage basin. Tributaries are changed from Class I to II and II to III, as fewer and shorter portions of a stream system can support cold-water adapted fish or amphibians.

Effects of Forest Practices on Stream Biota

Most aquatic organisms have not been studied thoroughly enough to document impacts on their populations from human activities. For the several species discussed below, however, enough is known to make them potential indicators of the ecological condition of streams.

THE SOUTHERN TORRENT SALAMANDER. The southern torrent salamander may be more tolerant of stream canopy removal in the marine-influenced coastal redwood zone than elsewhere, based on its present distribution on altered landscapes (Diller and Wallace 1996). Nevertheless, declines on commercial timberlands may proceed undetected because the presence of individuals at some harvested sites is considered evidence of population persistence without any testing of this assumption (e.g., Brode 1995). Torrent salamander spatial distributions (metapopulation structure) and densities on managed redwood timberlands have never been compared with those of nearby pristine parklands. Data for this

species from commercial timberlands need to be compared with data from reference sites to test the assumption that the torrent salamander is protected sufficiently by current forestry rules.

We found a mean density of 0.372 salamanders/m² (S.E. 0.0039) in five pristine streams in Prairie Creek Redwoods State Park in Humboldt County (Welsh and Ollivier 1998). Although we were not able to obtain comparable density data to compare with data from our reference sites, we did find relative abundance data (captures/unit of search effort) from Pacific Lumber Company lands in Humboldt County, California (Wroble and Waters 1989). Wroble and Waters (1989) reported an average of 0.052 southern torrent salamanders/hour of search time (S.D. 0.092) from seventeen streams on Pacific Lumber lands. For our comparison, we took a liberal approach (one that would tend to favor the timber company) by including data from all ten streams in our study (Welsh and Ollivier 1998), which included five affected streams (those with an infusion of fine sediments from a storm-triggered, road-building-related slope failure) and five pristine streams. We still found an average of 0.724 southern torrent salamanders/hour (S.D. 0.786) in the ten streams sampled at Prairie Creek—a highly significant difference (Mann-Whitney test; $Z = 2.93$, $p = 0.003$) (Welsh and Ollivier, unpub. data).

Diller and Wallace (1996) argued that torrent salamander distributions on commercial timberlands were determined by the gradient of the stream channel. Their argument was that stream channels with steeper gradients generate higher water velocities, which tend to flush fine sediments from the coarse substrates and thus create better microhabitat for this salamander. We agree with the general process model they describe (i.e., flushing of coarse substrates creates better microhabitat); however, we disagree that it follows that steeper channels are therefore required to support salamanders. Though this may be the case on commercial timberlands (Diller and Wallace 1996), interpretation of the data suggests that much of the suitable microhabitat along streams with gentle gradients has been compromised by excessive fine sediments in the streambed substrate on managed lands. To test this hypothesis, we examined our data from the ten reference streams in late-seral redwood forest at Prairie Creek Redwoods State Park (Welsh and Ollivier 1998). For those stream habitat units (e.g., pools, riffles, runs) with salamanders, we found a range of channel gradient from 2-14 percent ($n = 26$ stream habitat units; Welsh and Ollivier, unpub. data). We found no statistically significant correlation between channel gradient and salamanders ($r = -0.213$, $p = 0.295$).

Wroble and Waters (1989) proposed that low numbers of southern torrent salamanders on commercial timberlands are the result of a parent geology that is unconsolidated and naturally yields high levels of fine sediments, making streambed substrates unsuitable for torrent salamanders on these lands. This argument fails when considering that the streams with abundant populations of

torrent salamanders in Prairie Creek Redwoods State Park also dissect an unconsolidated parent geology. To examine this question, we tested the hypothesis that parent geology influences the occurrence of populations of this salamander, using all available locality data from across the range in northwestern California ($N = 83$ sites; Redwood Sciences Laboratory, unpub. data). We classified all 83 localities as to parent geology, using U.S. Geological Survey maps for northern California. The presence of torrent salamanders was independent of parent geology type (consolidated vs. unconsolidated) ($X^2 = 0.153$, $p = 0.696$; Welsh and Ollivier, unpub. data).

Welsh and Lind (1996) argued that current forestry rules are inadequate to protect this salamander because they fail to protect headwaters areas. The continued isolation and fragmentation of headwater habitats, and the minimal protections afforded these sensitive habitats under current forestry rules, could have significant negative genetic consequences for populations on commercial forestlands (Welsh and Lind 1996). Torrent salamanders display some of the highest genetic diversity among sibling populations ever documented for a vertebrate species (Good and Wake 1992), suggesting that fragmentation and isolation have long been a part of their evolutionary history. Movement studies (Welsh and Lind 1992) suggest that torrent salamanders are highly sedentary, which could partly explain the high genetic diversity observed among populations. Nevertheless, it is highly unlikely that isolating processes occurred at the current rate or across so much of the range of this species in the past. Few data exist to determine how much fragmentation and isolation this species can tolerate before going extinct, but there is some circumstantial evidence.

Multiyear sampling of aquatic vertebrates from Caspar Creek in Mendocino County failed to detect torrent salamanders (Nakamoto 1998), although this drainage is well within the species' range and contains suitable habitat. Caspar Creek was splash-dam logged in the nineteenth century (Napolitano 1998); torrent salamander populations were likely extirpated by this activity and apparently have failed to recolonize in the intervening 100+ years. Evidence from the Mattole River suggests that anthropogenic disturbance has caused this species to decline across most of the watershed (Welsh et al., in prep.). Gene flow among the few remaining subpopulations is unlikely because of the limited amount of equable forest cover in the Mattole watershed. Further declines in late-seral habitats in the Mattole watershed will result in a high probability of the southern torrent salamander being extirpated from this watershed.

PACIFIC GIANT SALAMANDER. Although aquatic giant salamanders appear relatively impervious to some alterations of the near-stream environment (e.g., Murphy and Hall 1981; Murphy et al. 1981; Hawkins et al. 1983), their numbers can decline in response to habitat degradation resulting from sedimentation of the channel (see previous citations and Welsh and Ollivier 1998). They are

sufficiently widespread and abundant in streams of the redwood region that their numbers might serve as an indicator of relative stream quality. Welsh et al. (1997) reported high numbers of Pacific giant salamanders along a 1-km length of Little Lost Man Creek in Redwood National Park, with an estimated mean density of approximately one salamander/m² ($\bar{x}$ = 0.956; S.E. 0.170). Welsh and Ollivier (1998) found a mean density of 1.33 salamanders/m² (S.E. 0.0069) for five pristine streams in old-growth redwood forest at Prairie Creek Redwoods, inclusive of Little Lost Man Creek. Nakamoto (1998) found similar densities of Pacific giant salamanders in the north fork of Caspar Creek and slightly fewer in the south fork, but found no differences before and after logging in either drainage. We are unaware of comparable data from commercial timberlands. More research on the response of the Pacific giant salamander to stream habitat modifications are needed, given the conflicting results obtained by Nakamoto (1998) and Welsh and Ollivier (1998).

THE TAILED FROG. The tailed frog is associated with late-seral forest conditions in northern California; the species appears to be negatively affected by timber harvesting there (Welsh 1990, 1993) and in Oregon (Corn and Bury 1989). Recent evidence indicates that the tailed frog has declined in the Mattole Basin as a result of anthropogenic changes to the landscape (Welsh et al., in prep.). Nakamoto (1998) reported tailed frog larvae in the north fork of Caspar Creek, but apparently too few were present for a comparative analysis. He indicated that tailed frog larvae were absent in the more heavily altered south fork, which was logged in the nineteenth century and then again in the 1960s. On the other hand, salmonid abundances in the south fork of Caspar Creek appeared to have returned to near prelogging levels (Burns 1972 cited in Nakamoto 1998).

We found mean densities of 0.929 tailed frog tadpoles/m² (S.E. 0.265) in one kilometer of Little Lost Man Creek in Redwood National Park (Welsh and Ollivier, unpubl. data) and 1.01 tailed frog tadpoles/m² (S.E. 0.0008) in five pristine streams in old-growth redwood forest inclusive of Little Lost Man Creek (Welsh and Ollivier 1998). Using the liberal analysis approach described above, we converted our data from Prairie Creek Redwoods (Welsh and Ollivier 1998; all ten streams) to captures/unit of search effort, then compared our data with those from seventeen streams on Pacific Lumber Company lands (Wroble and Waters 1989). Wroble and Waters (1989) reported 0.108 tailed frogs/hour (S.D. 0.097). Our surveys yielded 2.40 tailed frogs/hour (S.D. 1.58), a significantly greater abundance of tailed frog tadpoles than occurred on the Pacific Lumber landscape (Mann-Whitney test; $Z = 4.30$, $p < 0.0001$; Welsh and Ollivier, unpub. data). Given that Pacific Lumber Company lands lie well within the range of this species, and streams in redwood forest in this region typically support high numbers of this frog, our conclusion from this comparison is that the

streams on Pacific Lumber Company lands are in exceptionally poor condition for tailed frogs as a result of timber harvesting.

THE FOOTHILL YELLOW-LEGGED FROG. The foothill yellow-legged frog is listed as a sensitive species by state and federal agencies based on dramatic declines of populations in California's Sierra Nevada foothills (see chap. 5, table 5.2). Populations of this frog appear to be stable in the redwood region, but they are highly susceptible to water diversions and channel alterations (e.g., gravel mining), which can interfere with their reproductive cycle, resulting in dramatic population crashes (Lind et al. 1996).

THE WESTERN POND TURTLE. The sedimentation of pools associated with timber harvesting, road building, and gravel mining probably have a negative effect on western pond turtle populations by reducing required habitats. Water diversions may also have negative influences on this turtle, particularly if they reduce the quality and amounts of shallow, warm-water microhabitats required as rearing areas by juvenile turtles (Reese and Welsh 1998).

Amphibians as Bioindicators

Their high relative abundances, sensitive physiology, and high site fidelity (relatively low mobility) make amphibians excellent candidates for bioindicators of ecosystem health. Welsh and Ollivier (1998) have tested this idea in streams of the redwood forest, where they documented significant adverse effects of increased fine sediments on three amphibian species (see fig. 6.6 a-c). Welsh et al. (in prep.) demonstrated a link between low stream temperatures, mature forest cover along the riparian zone, and the presence of cold-water adapted amphibians (i.e., the tailed frog and the southern torrent salamander) in the Mattole watershed of northern California.

Of the native stream amphibians of the redwood region, tailed frogs may be the most sensitive to anthropogenic perturbations. The larval stage, in particular, has great potential as an ecological indicator (Welsh and Ollivier 1998). Larval tailed frogs, along with the southern torrent and Pacific giant salamanders, are logical surrogates for gauging habitat conditions for anadromous fishes, such as coho and Chinook salmon, because they are long-lived, highly philopatric, and require very similar stream microhabitat conditions, such as clean gravels and cold water temperatures (Welsh and Ollivier 1998). Data on amphibian densities from reference stream habitats in pristine redwood forests have the potential to serve as a benchmark against which to compare densities in streams on managed lands. These data could also be used to generate indices of the relative condition ("health") of managed streams and to establish threshold targets for recovery efforts as proposed by Welsh and Ollivier (1998). Studies of stream amphibian densities are needed across all of the redwood parklands to establish the natural range of variability for these sentinel species.

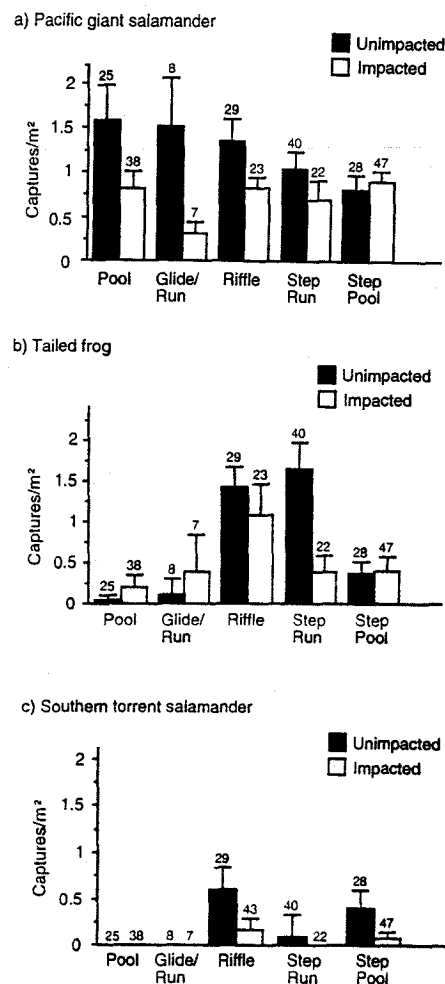


Figure 6.6. a-c. Densities of three species of amphibians with respect to stream habitat type and anthropogenic stress of fine sediment infusion (impacted). Data from five impacted and five unimpacted tributary streams in the Prairie Creek watershed, Prairie Creek State Redwoods. (From Welsh and Ollivier 1998.)

Research Needs

Several recent publications provide excellent reviews of current knowledge of stream ecology and terrestrial/aquatic linkages in the Pacific Northwest (Meehan 1991; FEMAT 1993; Spence et al. 1996; NRC 1996; Stouder et al. 1997; Naiman and Bilby 1998). Nevertheless, little integrated, holistic research on stream ecosystems has been carried out in the redwood region (but see Ziemer 1998b). This shortcoming can be explained by the enormous complexity of

aquatic ecosystems, resistance within scientific disciplines to integrated interdisciplinary research (Regier 1978; Bella 1987), lack of funding for extensive research, and the private ownership of most of the region. Even the few pristine streams in public ownership (primarily state and national parks) are poorly studied. Although anadromous salmonids probably are the most thoroughly studied aquatic organisms in the redwood region, knowledge of their historic and current populations is limited. The observations of renowned Stanford University ichthyologist John Snyder (1925) still apply:

It may not be out of place here to call attention to the well-known fact that stream fishing for trout, a major sport in California, is rapidly entering a critical stage. The extension of roads easily negotiated by the automobile, the building of high dams, the netting of steelheads in the rivers, water pollution, the use of water for irrigation, and many other things incident to a rapid growth in population are causing a marked and sudden depletion in the number of fish. It has been said that intelligent conservation must depend largely on our knowledge of the natural history of the species, and nowhere else is this more applicable. Very often our attempts at conservation serve among other things to bring to the surface our lack of definite knowledge of the habits and life history of the very fish that we are striving to protect. It is to be hoped that active support will be given to the Fish and Game Commission in every effort at careful investigation along this line.

We know little about the competitive and other interactions between salmonids and other aquatic organisms. Wilson and Halupka (1995) regarded anadromous fish as keystone species within vertebrate communities, yet nothing is known about the community effects of the drastic declines in salmonid populations throughout the redwood region. The loss of nutrients formerly brought in from the ocean by salmon (Bilby et al. 1996) undoubtedly has altered stream and riparian ecosystems, yet the magnitude or direction of change is unknown. Microbial dynamics in nutrient cycling and spiraling, although certainly a vital part of stream community structure and function, are virtually unstudied in the redwood region.

Research is urgently needed on exotic species introductions in the streams and rivers of the redwood region. Several predator species have been introduced into aquatic systems, and the potential influences on native species could be serious. For example, the predator Sacramento squawfish has been introduced into the Eel River system (Brown and Moyle 1997), as has the bullfrog (Kupferburg 1994), a voracious predator on other amphibians, reptiles, birds, and small mammals. The bullfrog has also recently been detected in the Mattole River (H. Welsh, pers. obs.).

Conclusions

In this chapter we have reviewed the available science on the processes and functions of riparian and aquatic ecosystems in the redwood region, along with the evidence of anthropogenic effects on these systems. Our impression is that, collectively, these studies support the notion that "the retention, restoration, and protection of aquatic and riparian processes and landforms that contribute habitat elements to streams and promote good habitat conditions for fish and other aquatic and riparian-dependent organisms" (Sedell et al. 1994) are essential to maintaining a functioning aquatic ecosystem and healthy, populations of these resources across the landscape in perpetuity. Much work remains to be done to reverse the decline of the aquatic and riparian ecosystem in the redwood region. We are all stakeholders.

Appendix 6.I. Plant and Vertebrate Species Associated with Aquatic Ecosystems of the Redwood Region.

<i>Common Name</i>	<i>Scientific Name</i>	<i>Common Name</i>	<i>Scientific Name</i>
Alder	<i>Alnus spp.</i>	Long-eared bat	<i>Myotis evotis</i>
Red alder	<i>Alnus rubra</i>	Yuma myotis	<i>Myotis yumanensis</i>
Big-leaf maple	<i>Acer macrophyllum</i>	Hoary bat	<i>Lasiurus cinereus</i>
Willow	<i>Salix spp.</i>	Silver-haired bat	<i>Lasionycteris noctivagans</i>
Osprey	<i>Pandion haliaetus</i>	Pacific giant	<i>Dicamptodon tenebrosus</i>
Bald eagle	<i>Haliaeetus leucocephalus</i>	salamander	
Belted kingfisher	<i>Ceryle alcyon</i>	California giant	<i>Dicamptodon ensatus</i>
American dipper	<i>Cinclus mexicanus</i>	salamander	
Great blue heron	<i>Ardea herodias</i>	Southern torrent	<i>Rhyacotriton variegatus</i>
Green heron	<i>Butorides virescens</i>	salamander	
Common	<i>Mergus merganser</i>	Northwestern	<i>Ambystoma gracile</i>
merganser		salamander	
Killdeer	<i>Charadrius vociferus</i>	Rough-skinned	<i>Taricha granulosa</i>
Spotted	<i>Actitis macularia</i>	newt	
sandpiper		Red-bellied newt	<i>Taricha rivularis</i>
River otter	<i>Lutra canadensis</i>	Pacific tree frog	<i>Hyla regilla</i>
Mink	<i>Mustela vison</i>	Yellow-legged frog	<i>Rana boylei</i>
Muskrat	<i>Ondatra zibethicus</i>	Tailed frog	<i>Ascaphus truei</i>
Raccoon	<i>Procyon lotor</i>	Western toad	<i>Bufo boreas</i>
Black bear	<i>Ursus americanus</i>	Northwestern	<i>Clemmys marmorata</i>
California myotis	<i>Myotis californicus</i>	pond turtle	
Little brown bat	<i>Myotis lucifugus</i>	Oregon aquatic	<i>Thamnophis atratus</i>
Long-legged bat	<i>Myotis volans</i>	garter snake	

Literature Cited

- Allan, J. D. 1995. *Stream ecology: Structure and function of running waters*. London: Chapman and Hall.
- Andrus, E. W. 1988. Woody debris and its contribution to pool formation in a coastal stream fifty years after logging. *Canadian Journal of Fisheries and Aquatic Sciences* 45:2080-2086.
- Bella, D. A. 1987. Ethics and the credibility of applied science. Pp. 19-32 in G. H. Reeves, D. L. Bottom, and M. H. Brookes, coordinators, *Ethical questions for resource managers*, Portland, OR: USDA Forest Service General Technical Report PNW-GTR-288.
- Bencala, K. E. 1984. Interactions of solutes and streambed sediments II: A dynamic analysis of coupled hydrologic and chemical process that determine solute transport. *Water Resources Research* 20:1804-1814.
- Beschta, R. L., R. E. Bilby, G. W. Brown, L. B. Holtby, and T. D. Hofstra. 1987. Stream temperature and aquatic habitat: Fisheries and forestry interactions. Pp. 199-232 in E. O. Salo and T. W. Cundy, eds., *Streamside management: Forestry and fishery interactions*. Contribution no. 57. Seattle, WA: Institute of Forest Resources, University of Washington.
- Bilby, R. E., B. R. Fransen, and P. A. Bisson. 1996. Incorporation of nitrogen and carbon from spawning coho salmon into the trophic systems of small streams: Evidence from stable isotopes. *Canadian Journal of Fisheries and Aquatic Sciences* 53:164-173.
- Bormann, F. H., and G. E. Likens. 1979. *Patterns and process in a forested ecosystem*. New York, NY: Springer-Verlag.
- Boulton, A. J., and P. S. Lake. 1991. Benthic organic matter and detritivorous macroinvertebrates in two intermittent streams in south-eastern Australia. *Hydrobiologia* 241:107-118.
- Brode, J. 1995. Status review of the southern torrent salamander (*Rhyacotriton variegatus*) in California. Rancho Cordova, CA: California Department of Fish and Game Report.
- Broszofski, K. B., J. Chen, R. J. Naiman, and J. F. Franklin. 1997. Harvesting effects on microclimatic gradients from small streams to uplands in western Washington. *Ecological Applications* 7:1188-1200.
- Brown, L. R., and P. B. Moyle. 1997. Invading species in the Eel River, California: Successes, failures, and relationships with resident species. *Environmental Biology of Fishers* 49:271-291.
- Brown, L. R., P. B. Moyle, and R. M. Yoshiyama. 1994. Historical decline and current status of coho salmon in California. *North American Journal of Fisheries Management* 14(2):237-261.
- Burns, J. W. 1992. Some effects of logging and associated road construction on northern California streams. *Trans. Amer. Fish. Soc.* 101:1-17.
- Busby, P. J., T. C. Wainwright, and R. S. Waples. 1994. Status review for Klamath Mountain province steelhead. U.S. Dept. Commerce, NOAA Technical Memorandum NMFS-NWFSC-19.
- Cederholm, C. J., D. B. Houston, D. L. Cole, and W. J. Scarlett. 1989. Fate of coho salmon (*Oncorhynchus kisutch*) carcasses in spawning streams. *Canadian Journal of Fisheries and Aquatic Sciences* 46:1347-1355.
- Corn, P. S., and R. B. Bury. 1989. Logging in western Oregon: Responses of headwater habitats and stream amphibians. *Forest Ecology and Management* 29:39-57.
- Cummins, K. W. 1974. Structure and function of stream ecosystems. *BioScience* 24:631-641.

- Cummins, K. W., and M. J. Klug. 1979. Feeding ecology of stream invertebrates. *Annual Review of Ecology and Systematics* 20:147-172.
- Diller, L. V., and R. L. Wallace. 1994. Distribution and habitat of *Plethodon elongates* on managed, young growth forests in north coastal California. *Journal of Herpetology* 28:310-318.
- _____. 1996. Distribution and habitat of *Rhyacotriton variegatus* on managed, young growth forests in north coastal California. *Journal of Herpetology* 30:184-191.
- Dahm, C. N. 1981. Pathways and mechanisms for removal of dissolved organic carbon from leaf leachate in streams. *Canadian Journal of Fisheries and Aquatic Sciences* 38:68-76.
- Daugherty, C. H., and A. L. Sheldon. 1982a. Age-determination, growth, and life-history of a Montana population of the tailed frog, *Ascaphus truei*. *Herpetologica* 38:461-468.
- _____. 1982b. Age-specific movement patterns of the tailed frog, *Ascaphus truei*. *Herpetologica* 38:468-474.
- Dill, W. A., and A. J. Cordone. 1997. *History and status of introduced fishes in California, 1871-1996*. Fish Bulletin 178. Sacramento, CA: California Dept. of Fish and Game.
- Duff, J. H., and F. J. Triska. 1990. Denitrification in sediments from the hyporheic zone adjacent to a small forested stream. *Canadian Journal of Fisheries and Aquatic Science* 47:1140-1147.
- FEMAT (Forest Ecosystem Management Assessment Team). 1993. *Forest ecosystem management: An ecological, economic, and social assessment*. Report of the Forest Ecosystem Management Assessment team, Portland, OR: USDA Forest Service.
- Frissell, C. A. 1992. Cumulative effects of land use on salmon habitat in southwest Oregon coastal streams. Ph.D. diss., Oregon State University, Corvallis, OR.
- Frissell, C. A., and D. Bayles. 1996. Ecosystem management and the conservation of aquatic biodiversity and ecological integrity. *Water Resources Bulletin* 32:229-240.
- Frissell, C. A., W. J. Liss, R. E. Gresswell, R. K. Nawa, and J. L. Ebersole. 1997. A resource in crisis: Changing the measure of salmon management. Pp. 411-444 in D. J. Stouder, P. A. Bisson, and R. J. Naiman, eds., *Pacific salmon the their ecosystems: Status and future options*. New York, NY: Chapman and Hall.
- Fuller, D. D., and A. J. Lind. 1992. Implications of fish habitat improvement structures for other stream vertebrates. Pp. 96-104 in R. R. Harris and D. E. Erman, tech. coordinators, and H. M. Kemer, ed., *Proceedings of the symposium on biodiversity of north-western California*. October 28-30, 1991, Santa Rosa, California. Wildland Resource Center Report 29. Berkeley: University of California.
- Gates, J. H. 1993. *Falk's claim: The life and death of a redwood lumber town*. Eureka, CA: Pioneer Graphics.
- Gerstung, E. R. 1997. Status of coastal cutthroat trout in California. Pp. 43-56 in J. D. Hall, P. A. Bisson, and R. E. Gresswell, eds., *Sea-run cutthroat trout: Biology, management, and future conservation*. Corvallis, OR: Oregon Chapter, American Fisheries Society.
- Good, D. A. 1989. Hybridization and cryptic species in *Dicamptodon* (Caudata: Dicamptodontidae). *Evolution* 43:728-744.
- Good, D. A., and D. B. Wake. 1992. Geographic variation and spciation in the torrent salamanders of the genus *Rhyacotriton* (Caudata: Rhyacotritonidae). University of California Publications in Zoology 126, 91 pp.
- Gregory, S. V., G. A. Lamberti, and K. M. S. Moore. 1989. Influence of valley floor landforms on stream ecosystems. Pp. 3-9 in D. L. Abell, ed., *Proceedings of the California Riparian Systems Conference: Protection, management, and restoration for the 1990's*. September 22-24, 1988, Davis, CA. General Technical Report PSW-110,

Pacific Southwest Forest and Range Experiment Station, Berkeley, CA: USDA Forest Service.

- Gregory, S. V., F. J. Swanson, W. A. McKee, and K. W. Cummins. 1991. An ecosystem perspective of riparian zones. *Bioscience* 41(8): 540-551.
- Grimm, N. B., and S. G. Fisher. 1984. Exchange between interstitial and surface water: Implications for stream metabolism and nutrient cycling. *Hydrobiologia* 111:219-228.
- Hagans, D. K., and W. E. Weaver. 1987. Magnitude, cause and basin response to fluvial erosion, Redwood Creek basin, northern California. Pp. 419-428 in R. L. Beschta, T. Blinn, G. E. Grant, G. G. Ice, and F. J. Swanson, eds., *Erosion and sedimentation in the Pacific Rim*. International Association of Hydrological Sciences Publication No. 165.
- Harrington, J. M. 1983. An evaluation of techniques for collection and analysis of benthic invertebrate communities in second order streams in Redwood National Park. Master's thesis, Humboldt State University, Arcata, CA.
- Hawkins, C. P., K. L. Murphy, H. H. Anderson, and M. A. Wilzbach. 1983. Density of fish and salamanders in relation to riparian canopy and physical habitat in streams of the northwestern United States. *Canadian Journal of Fish and Aquatic Sciences* 40:1173-1185.
- Healey, M. C. 1991. Life history of Chinook salmon (*Oncorhynchus tshawytscha*). Pp. 313-393 in C. Groot and L. Margolis, eds., *Pacific salmon life histories*. Vancouver, BC: University of British Columbia Press.
- Hicks, B. J., J. D. Hall, P. A. Bisson, and J. R. Sedell. 1991. *Responses of salmonids to habitat changes*. American Fisheries Society Special Publication 19:483-5118.
- Holt, R. D., and M. S. Gaines. 1992. Analysis of adaptation in heterogeneous landscapes: The manifold role of habitat selection. *Evolution and Ecology* 1992:433-447.
- Iwatsubo, R. T., and R. C. Averett. 1981. Aquatic biology of the Redwood Creek and Mill Creek drainage basins. Redwood National Park Humboldt and Del Norte Counties, California. U.S. Geological Survey Open File Report 81-143.
- Iwatsubo, R. T., K. M. Nolan, D. R. Harden, and G. D. Glysson. 1976. Redwood National Park studies, data release number 2, Redwood Creek, Humboldt County, and Mill Creek, Del Norte County, California, April 11, 1974-Sept. 30, 1975. U.S. Geological Survey Open-File Report 76-678.
- Iwatsubo, R. T., K. M. Nolan, D. R. Harden, G. D. Glysson, and R. J. Janda. 1975. Redwood National Park studies, data release number 1, Redwood Creek, Humboldt County, and Mill Creek, Del Norte County, California, Sept. 1, 1973—April 10, 1974. U.S. Geological Survey Open-File Report.
- Janda, R. J., K. M. Nolan, D. R. Harden, and S. M. Coleman. 1975. Watershed conditions in the drainage of Redwood Creek, Humboldt County, California, as of 1973. U.S. Geological Survey, Open File Report 75-568, Menlo Park, CA.
- Karraker, N. E., and G. S. Beyersdorf. 1997. A tailed frog (*Ascaphus truei*) nest site in northwestern California. *Northwestern Naturalist* 78:110-111.
- Keller, E. A., A. MacDonald, T. Tally, and N. J. Merrit. 1995. Effects of large organic debris on channel morphology and sediment storage in selected tributaries of Redwood Creek, northwestern California. Pp. 1-29 in K. M. Nolan, H. M. Kelsey, and D. C. Marron, eds., *Geomorphic processes and aquatic habitats in the Redwood Creek Basin, northwestern California*. U.S. Geological Survey Professional Paper 1454-P. Washington, DC: U.S. Government Printing Office.
- Kelsey, H. M. 1980. A sediment budget and an analysis of geomorphic process in the Van Duzen River basin, north coastal California, 1941-1975. *Geological Society of America Bulletin* 91:119-1216.

- Keppeler, E. T. 1998. The summer flow and water yield response to timber harvest. Pp. 37-46 in R. Ziemer, ed., *Proceedings of the conference on coastal watersheds: The Caspar Creek story*. USDA FS PS-GTR 165.
- Keppeler, E. T., D. Brown. 1998. Subsurface drainage processes and management impacts. Pp. 25-35 in R. Ziemer, ed., *Proceedings of the conference on coastal watersheds: The Caspar Creek story*. USDA FS PS-GTR 165.
- Kupferberg, S. J. 1994. Exotic larval bullfrogs (*Rana catesbeiana*) as prey for native garter snakes: Functional and conservation implications. *Herpetological Review* 25(3): 95-97.
- Laurance, W. F., and E. Yensen. 1990. Predicting the impacts of edge effects in fragmented habitats. *Biological Conservation* 55:77-92.
- Ledwith, T. 1996. The effects of buffer strip width on air temperature and relative humidity on a stream riparian zone. *Watershed Management Council Networker* 6(4): 6-7.
- Leonard, W. P., H. A. Brown, L. L. C. Hones, K. R. McAllister, and R. M. Storm. 1993. *Amphibians of Washington and Oregon*. Seattle, WA: Seattle Audubon Society.
- Lewis, J. 1998. Evaluating the impacts of logging activities on erosion and suspended sediment transport in the Caspar Creek Watersheds. Pp. 59-74 in R. Ziemer, ed., *Proceedings of the conference on coastal watersheds: The Caspar Creek story*. USDA FS PS-GTR 165.
- Lind, A.J., and H. H. Welsh Jr. 1990. Predation of *Thamnophis couchi* on *Dicamptodon ensatus*. *Journal of Herpetology* 24:104-106.
- _____. 1994. Ontogenetic changes in the foraging behavior and habitat use of the Oregon garter snake, *Thamnophis atratus hydrophilus*. *Animal Behavior* 48:1261-1273.
- Lind, A. J., H. H. Welsh Jr., and R. A. Wilson. 1996. The effects of a dam on breeding habitat and egg survival of the foothill yellow-legged frog (*Rana boylei*). *Herpetological Review* 27:62-67.
- Lisle, T. E. 1982. Effects of aggradation and degradation on riffle-pool morphology in natural gravel channels, northwestern California. *Water Resources Research* 18:1643-1651.
- _____. 1989. Channel-dynamic control on the establishment of riparian trees after large floods in northwestern California. Pp. 9-13 in D. L. Abell, ed., *Proceedings of the California riparian systems conference*. September 9-13, 1988. Berkeley, CA. USDA Forest Service General Technical Report PSW-110.
- Lisle, T. E., and M. B. Napolitano. 1998. Effects of recent logging on the main channel of North Fork Caspar Creek. Pp. 87-93 in R. Ziemer, ed., *Proceedings of the conference on coastal watersheds: The Caspar Creek story*. USDA FS PS-GTR 165.
- Madej, M. A. 1987. Residence times of channel-stored sediment in Redwood Creek, northwestern California. Pp. 429-438 in R. L. Beschta, T. Blinn, G. E. Grant, G. G. Ice, and F. J. Swanson, eds., *Erosion and sedimentation in the Pacific Rim*. International Association of Hydrological Sciences Publication No. 165, Wallingford, UK.
- Madej, M. A., and V. Ozaki. 1996. Channel response to sediment wave propagation and movement, Redwood Creek, California, USA. *Earth Surface Processes and Landforms* 21:911-927.
- Maser, C., R. F. Tarrant, J. M. Trappe, and J. F. Franklin, eds. 1988. *From the forest to the sea: A story of fallen trees*. U.S. Forest Service, Pacific Northwest Research Station PNW-GTR-229. Portland, OR: USDA Forest Service.
- Mattole Sensitive Watershed Group. 1996. A nomination from concerned citizens of the Mattole River Watershed of the State of California proposing the Mattole River as a

- sensitive watershed. Prepared for the California Board of Forestry and the California Department of Forestry, Sacramento, CA.
- Mayer, K. E., and W. F. Laudenslayer. 1988. *A guide to wildlife habitats of California*. Sacramento, CA: California Department of Forestry and Fire Protection.
- McGinnis, S. M. 1984. *Freshwater fishes of California*. Berkeley: University of California Press.
- McKenzie, M., S. T. Gellman, and W. J. Zielinski. 1994. Interim biological assessment of the proposed Wilson Creek realignment project route 101, Del Norte County, California. Report 01-DN-101-12.5/16.3. Eureka, CA: California Dept. Transportation.
- Meehan, W. R., ed. 1991. *Influences of forest and rangeland management on salmonid fishes and their habitats*. American Fisheries Society Special Publication 19.
- Merritt, R. W., and K. W. Cummins. 1978. *An introduction to the aquatic insects of North America*. Dubuque, IA: Kendall/Hunt.
- Minshall, G. W., R. C. Peterson, K. W. Cummins, T. L. Bott, J. R. Sedell, C. E. Cushing, and R. L. Vannote. 1983. Interbiome comparison of ecosystem dynamics. *Ecological Monographs* 51:1-25.
- Minshall, G. W., K. W. Cummins, R. C. Peterson, C. E. Cushing, D. A. Bruns, J. R. Sedell, and R. L. Vannote. 1985. Developments in stream ecosystem theory. *Canadian Journal of Fisheries and Aquatic Sciences* 42:1045-1055.
- Minshall, G. W., R. C. Peterson, T. L. Bott, C. E. Cushing, K. W. Cummins, R. L. Vannote, and J. R. Sedell. 1992. Stream ecosystem dynamics of the Salmon River, Idaho: An eighth order system. *Journal of the north American Benthological Society* 11(2):111-137.
- Mitchell, W. T. 1988. Microhabitat utilization and spatial segregation of juvenile coastal cutthroat and steelhead trout in the Smith River drainage, California. Master's thesis, Humboldt State University, Arcata, CA.
- Moyle, P. B. 1976. *Inland fishes of California*. Berkeley: University of California Press.
- Moyle, P. B., and B. Herbold. 1987. Life-history patterns and community structure in stream fishes of western North America: Comparisons with eastern North America and Europe. Pp. 25-32 in W. J. Matthews and D. C. Heins, eds., *Community and evolutionary ecology of North American stream fishes*. Norman: University of Oklahoma Press.
- Moyle, P. B., R. M. Yoshiyama, E. D. Wikramanayake, and J. W. Williams. 1995. *Fish of special concern*. 2d ed. Report to the California Department of Fish and Game. Sacramento, CA.
- MRC (Mattole Restoration Council). 1989. Elements of recovery: An inventory of up-lope sources of sedimentation in the Mattole River watershed. Report prepared by the MRC for the California Department of Fish and Game, Sacramento, CA.
- Mulholland, P. J. 1992. Regulation of nutrient concentrations in a temperate forest stream: Roles of upland, riparian, and instream processes. *Limnology and Oceanography* 37:1512-1526.
- Murphy, M. L., and J. D. Hall. 1981. Varied effects of clear-cut logging on predators and their habitats in small streams of the Cascade Mountains, Oregon. *Canadian Journal of Fisheries and Aquatic Sciences* 38:137-145.
- Murphy, M. L., C. P. Hawkins, and N. H. Anderson. 1981. Effects of canopy modification and accumulated sediment on stream communities. *American Fisheries Society* 110:469-478.
- Murphy, M. L., and W. R. Meehan. 1991. Stream ecosystems. *American Fisheries Society Special Publication* 19:17-46.
- Naiman, R. J., and R. E. Bilby. 1998. *River ecology and management: Lessons from the Pacific coastal ecoregion*. New York, NY: Springer Verlag.

- Naiman, R. J., and H. Decamps. 1997. The ecology of interfaces: Riparian zones. *Annual Review of Ecology and Systematics* 28:621-658.
- Naiman, R. J., T. J. Beechie, L. E. Benda, D. R. Berg, P. A. Bisson, L. H. McDonald, M. D. O'Connor, P. L. Olson, and E. A. Steel. 1992. Fundamental elements of ecologically healthy watershed in the Pacific Northwest coastal ecoregion. Pp. 127-188 in R. J. Naiman, ed., *Watershed management: Balancing sustainability and environmental change*. New York, NY: Springer-Verlag.
- Naiman, R. J., K. L. Fetherston, S. J. McKay, and J. Chen. 1998. Riparian forests. Pp. 289-323 in R. J. Naiman and R. E. Bilby, eds., *River ecology and management: Lessons from the Pacific coastal ecoregion*. New York, NY: Springer-Verlag.
- Nakamoto, R. J. 1988. Effects of timber harvest on aquatic vertebrates and habitat in the North Fork Caspar Creek. Pp. 95-104 in R. Ziemer, ed., *Proceedings of the conference on coastal watershed: The Caspar Creek story*. USDA FS PS-GTR 165.
- Napolitano, M. 1998. Persistence of historical logging impacts on channel form in main-stem North Fork Caspar Creek. Pp. 105-109 in R. Ziemer, ed., *Proceedings of the conference on coastal watersheds: The Caspar Creek story*. USDA FS PS-GTR 165.
- Newbold, J. D., P. J. Mullholland, J. W. Elwood, and R. V. O'Neill. 1982. Organic carbon spiralling in stream ecosystems. *Oikos* 38:26-272.
- NMFS (National Marine Fisheries Service). 1998. See listing at <http://www.nwr.noaa.gov>.
- NRC (National Research Council). 1996. *Upstream: Salmon and society in the Pacific Northwest*. Washington DC: National Academy Press.
- Nussbaum, R. A. 1969. The nest of the Olympic salamander, *Rhyacotriton olympicus*. *Herpetologica* 25:277-278.
- Omernik, J. M., and A. L. Gallant, eds. 1986. *Ecoregions of the Pacific Northwest*. EPA/600/3-86/033. Corvallis, OR: U.S. Environmental Protection Agency.
- Pacific Watershed Associates. 1998. Sediment source investigation and sediment reduction plan for the Bear Creek watershed, Humboldt County, California. Report Prepared for the Pacific Lumber Company, Scotia, CA.
- Packer, M. S. 1960. Bioclimatic influences on the breeding of *Taricha rivularis*. *Ecology* 41:509-517.
- Parker, M. S. 1994. Feeding ecology of stream-dwelling Pacific giant salamander larvae (*Dicamptodon tenebrosus*). *Copeia* 1994:705-718.
- Power, M. E. 1991. Shifts in the effects of tuft-weaving midges on filamentous algae. *American Midland Naturalist* 125:275-285.
- _____. 1992. Hydrologic and trophic controls of seasonal blooms in northern California rivers. *Archiv für Hydrobiologie* 125:385-410.
- Reese, D. A., and H. H. Welsh Jr. 1997. Utilization of terrestrial habitat by western pond turtles (*Clemmys marmorata*): Implications for management. Pp. 352-357 in J. Van Abbema, ed., *Proceedings: Conservation, restoration, and management of tortoises and turtles: An international conference*. New York, NY: New York Turtle and Tortoise Society.
- _____. 1998. Habitat use by western pond turtles in the Trinity River, California. *Journal of Wildlife Management* 62:842-853.
- Reeves, G. H., L. E. Benda, K. M. Burnett, P. A. Bisson, and J. R. Sedell. 1995. A disturbance-based ecosystem approach to maintaining and restoring fresh-water habitats of evolutionarily significant units of anadromous salmonids in the Pacific Northwest. *American Fisheries Society Symposium* 17:334-349.
- Reeves, G. H., P. A. Bisson, and J. M. Dambacher. 1998. Fish communities. Chap. 9 in R. J. Naiman and R. E. Bilby, eds., *River Ecology and management: Lesson from the Pacific coastal ecoregion*. New York: Springer Verlag.

- Regier, H. A. 1978. *A balanced science of renewable resources with particular reference to fisheries*. Seattle: University of Washington Press.
- Reid, L. M., and S. Hilton. 1998. Buffering the buffer. Pp. 75-85 in R. Ziemer, ed., *Proceedings of the conference on coastal watersheds: The Caspar Creek story*. USDA FS PS-GTR 165.
- Resh, et al. 1988. The role of disturbance in stream ecology, *Journal of the North American Benthological Society* 7:433-455.
- Roelofs, T. D. 1983. Current status of California summer steelhead (*Salmo gairdneri*) stocks and habitat, and recommendation for their management. Report to USDA Forest Service Region 5.
- Sandercock, R. K. 1991. Life history of coho salmon (*Oncorhynchus kisutch*). Pp. 395-445 in C. Groot and L. Margolis, eds., *Pacific salmon life histories*. Vancouver: University of British Columbia Press.
- Saunders, D. A., R. J. Hobbs, and C. R. Margules. 1991. Biological consequences of ecosystem fragmentation: A review. *Conservation Biology* 5:18-32.
- Schlosser, T. D. 1991. Stream fish ecology: A landscape perspective. *BioScience* 41:704-712.
- Sedell, J. R., P. A. Bisson, F. J. Swanson, and S. V. Gregory. 1988. What we know about large trees that fall into streams and rivers. Pp. 47-81 in C. Maser, R. F. Tarrant, J. M. Trappe, and J. F. Franklin, eds., *From the forest to the sea: A story of fallen trees*. Pacific Northwest Research Station PNW-GTR-229. Portland, OR: USDA Forest Service.
- Sedell, J. R., G. H. Reeves, and K. M. Burnett. 1994. Development and evaluation of aquatic conservation strategies. *Journal of Forestry* 92(4):28-31.
- Sedell, J. R., G. H. Reeves, and P. A. Bisson. 1997. Habitat policy for salmon in the Pacific Northwest. Pp. 375-387 in D. J. Stouder, P. A. Bisson, and R. J. Naiman, eds., *Pacific salmon and their ecosystems: Status and future options*. New York, NY: Chapman and Hall.
- Semlitsch, R. D., D. E. Scott, J. H. K. Pechmann, and J. W. Gibbons. 1993. Phenotypic variation in the arrival time of breeding salamanders: Individual repeatability and environmental influences. *Journal of animal Ecology* 62:334-340.
- Shapovalov, L., and A. C. Taft. 1954. The life histories of the steelhead rainbow trout (*Salmo gairdneri gairdneri*) and silver salmon (*Oncorhynchus kisutch*) with special reference to Waddell Creek, California, and recommendations regarding their management. California Department of Fish and Game Fish Bulletin No. 98.
- Sidle, R. C., A. J. Pearce, and C. L. O'Loughlin. 1985. *Hillslope stability and land use*. Water Resources Monograph Series, vol. 11. Washington, DC: American Geophysical Union.
- Snyder, J. 1925. The half-pounder of Eel River, a steelhead trout. *California Fish and Game* 11(2):49-55.
- Southwood, T. R. E. 1977. Habitat, the templet for ecological strategies? *Journal of Animal Ecology* 46:337-365.
- Spence, B. C., G. A. Lomnický, R. M. Hughes, and R. P. Novitzki. 1996. *An ecosystem approach to salmonids conservation*. TR-4501-96-6057. Corvallis, Oregon: ManTech Environmental Research Services Corp.
- Stanford, J. A., and J. V. Ward. 1988. The hyporheic habitat of river ecosystems. *Nature* 335:64-66.
- _____. 1992. Management of aquatic resources in large catchments: Recognizing interactions between ecosystem connectivity and environmental disturbance. Pp. 91-124 in R. J. Naiman, ed., *Watershed management: Balancing sustainability and environmental change*. New York, NY: Springer-Verlag

- Stebbins, R. C. 1985. *A field guide to western reptiles and amphibians*. Boston, MA: Houghton Mifflin.
- Stouder, D. J., P. A. Bisson, and R. J. Naiman, eds. 1997. *Pacific salmon and their ecosystems*. New York, NY: Chapman and Hall.
- Strahler, A. N. 1957. Quantitative analysis of watershed geomorphology. *Transactions of the American Geophysical Union* 38(6):913-920.
- Townsend, C. R. 1989. The patch dynamics concept of stream community ecology. *Journal of the North American Benthological Society* 8:36-50.
- Triska, F. J., V. C. Kennedy, R. J. Avanzino, G. W. Zellweger, and K. E. Bencala. 1989a. Retention and transport of nutrients in a third-order stream in northwestern California: Hyporheic processes. *Ecology* 70:1877-1892.
- _____. 1989b. Retention and transport of nutrients in a third-order stream: Channel process. *Ecology* 70:1877-1892.
- Trotter, P. C. 1997. Sea-run cutthroat trout: Life history profile. Pp. 7-15 in J. D. Hall, P. A. Bisson, and R. E. Gresswell, eds., *Sea-run cutthroat trout: Biology, management, and future conservation*. Corvallis, OR: Oregon Chapter, American Fisheries Society.
- Twitty, V. C. 1964. *Taricha rivularis* (Twitty), red-bellied newt. *Catalogue of American Amphibians and Reptiles* 9.1-9.2.
- Vannote, R. L., G. W. Minshall, G. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences* 37:130-137.
- Veirs, S. D. 1982. Coast redwood forest: Stand dynamics, successional status, and the role of the fire. Pp. 119-141 in J. E. Means, ed., *Forest succession and stand development research in the northwest*. Corvallis, OR: Forest Research Laboratory, Oregon State University.
- Yahner, R. H. 1988. Changes in wildlife communities near edges. *Conservation Biology* 2:333-339.
- Yount, J. D., and G. J. Niemi. 1990. Recovery of lotic communities and ecosystems from disturbance: A narrative review of case studies. *Environmental Management* 14:547-570.
- Waide, J. B. 1995. Ecosystem stability: Revision of the resistance-resilience model. Pp. 372-396 in B. C. Patten and S. E. Jorgensen, eds., *Complex ecology: The part-whole relation in ecosystems*. Englewood Cliffs, NJ: Prentice Hall.
- Ward, J. V. 1994. The structure and dynamics of lotic ecosystems. Pp. 195-218 in R. Margalef, ed., *Limnology now: A paradigm of planetary problems*. Amsterdam: Elsevier.
- Weaver, W. E., D. K. Hagans, and J. H. Popenoe. 1995. Magnitude and causes of gully erosion in the lower Redwood Creek drainage basin. Pp. 11-121 in K. M. Nolan, H. M. Klesey, and D. C. Marron, eds., *Geomorphic processes and aquatic habitat in Redwood Creek Basin, northwestern California*. U.S. Geological Survey Professional Paper 1454. Washington, DC: Government Printing Office.
- Welsh, H. H., Jr. 1990. Relictual amphibians and old-growth forests. *Conservation Biology* 4:309-319.
- _____. 1993. A hierarchical analysis of the niche relationships of four amphibians from forested habitats of northwestern California. Ph.D. diss., University of California, Berkeley.
- Welsh, H. H., Jr., and A. J. Lind. 1992. Population ecology of two relictual salamanders from the Klamath Mountains of northwestern California. Pp. 419-437 in D. R. McCullough and R. H. Barrett, eds., *Wildlife 2001: Populations*. London: Elsevier.

- _____. 1996. Habitat correlates of the southern torrent salamander (*Rhyacotriton variegatus*) (Caudata: Rhyacotritonidae) in northwestern California. *Journal of Herpetology* 30:385-398.
- Welsh, H. H., Jr., L. M. Ollivier, and D. G. Hankins. 1997. A habitat-based design for sampling and monitoring stream amphibians with an illustration from Redwood National Park. *Northwestern Naturalist* 78:1-116.
- Welsh, H. H., Jr., and L. M. Ollivier. 1998. Stream amphibians as indicators of ecosystem stress: A case study from California's redwoods. *Ecological Applications* 8:1118-1132.
- Wemple, B. C., and J. A. Jones. 1996. Channel network extension by logging roads in two basins, western Cascades, Oregon. *Water Resources Bulletin* 32:1195-1207.
- Wilson, M. F., and K. C. Halupka. 1995. Anadromous fish as keystone species in vertebrate communities. *Conservation Biology* 1:344-345.
- Wootton, J. T., M. S. Parker, and M. E. Power. 1996. Effects of disturbance on river food webs. *Science* 273: 1558-1561.
- Wroble, J., and D. Waters. 1989. Summary of tailed frog (*Ascaphus truei*) and Olympic salamander (*Rhyacotriton olympicus variegatus*) stream surveys for the Pacific Lumber Company, October 1987 to September 1988. Report submitted to Pacific Lumber Co., January 9, 1989.
- Yoshiyama, R. M., F. W. Fisher, and P. B. Moyle. 1998. Historical abundance and decline of Chinook salmon in the Central Valley Region of California. *North American Journal of Fisheries Management* 18(3):487-521.
- Ziemer, R. R. 1998a. Flooding and stormflows. Pp. 15-24 in R. Ziemer, ed., *Proceedings of the conference on coastal watersheds: The Caspar Creek story*. USDA FS PS-GTR 165.
- Ziemer, R. R. 1998b. *Proceedings of the conference on coastal watersheds: The Caspar Creek story*. USDA FS PS-GTR 165.
- Ziemer, R. R., and T. E. Lisle. 1998. Hydrology. Pp. 43-68 in R. J. Naiman and R. E. Bilby, eds., *River ecology and management: Lessons from the Pacific Coastal Ecoregion*. New York, NY: Springer Verlag.
- Zweifel, R. G. 1955. Ecology, distribution, and systematics of frogs of the *Rana boylii* group. *University of California Publications in Zoology* 54:207-292.