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A Disturbance-Based Ecosystem Approach to Maintaining and Restoring Freshwater Habitats of Evolutionarily Significant Units of Anadromous Salmonids in the Pacific Northwest

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Abstract.—To preserve and recover evolutionarily significant units (ESUs) of anadromous salmonids *Oncorhynchus* spp. in the Pacific Northwest, long-term and short-term ecological processes that create and maintain freshwater habitats must be restored and protected. Aquatic ecosystems throughout the region are dynamic in space and time, and lack of consideration of their dynamic aspects has limited the effectiveness of habitat restoration programs. Riverine–riparian ecosystems used by anadromous salmonids were naturally subjected to periodic catastrophic disturbances, after which they moved through a series of recovery states over periods of decades to centuries. Consequently the landscape was a mosaic of varying habitat conditions, some that were suitable for anadromous salmonids and some that were not. Life history adaptations of salmon, such as straying of adults, movement of juveniles, and high fecundity rates, allowed populations of anadromous salmonids to persist in this dynamic environment. Perspectives gained from natural cycles of disturbance and recovery of the aquatic environment must be incorporated into recovery plans for freshwater habitats. In general, we do not advocate returning to the natural disturbance regime, which may include large-scale catastrophic processes such as stand-replacing wildfires. This may be an impossibility given patterns of human development in the region. We believe that it is more prudent to modify human-imposed disturbance regimes to create and maintain the necessary range of habitat conditions in space (10^3 km) and time (10^1–10^2 years) within and among watersheds across the distributional range of an ESU. An additional component of any recovery plan, which is imperative in the short-term, is the establishment of watershed reserves that contain the best existing habitats and include the most ecologically intact watersheds.

> Biodiversity is not a 'set-aside' issue that can be physically isolated in a few, or even many, reserves. . . . We must see the larger task—stewardship of all the species on all of the landscape with every activity we undertake as human beings—a task without spatial and temporal boundaries. (J. F. Franklin 1993)

Agencies responsible for the development of recovery plans for evolutionarily significant units (ESUs; Waples 1991) of anadromous salmonids *Oncorhynchus* spp. in the Pacific Northwest (PNW) of the United States face difficult tasks. First is the identification of ESUs. Second is the identification of factors that contribute to the decline of a particular ESU. A suite of factors, including habitat loss and degradation, overexploitation in sport and commercial fisheries, variable ocean conditions, and effects of hatchery practices, are responsible for the depressed status of these fish (Nehlsen et al. 1991). The relative importance of each in contributing to the decline of an ESU undoubtedly varies across the region. Any recovery program must address and incorporate consideration of all responsible factors to be successful.

The most common factor associated with declines of anadromous salmonids is habitat degradation, which includes destruction and modification of freshwater and estuarine habitats (Nehlsen et al. 1991; Frissell 1993). Stream and river systems

throughout the PNW have been extensively altered by human activities such as agriculture, urbanization, and timber harvest (Bisson et al. 1992). Features of altered ecosystems include changes (generally reductions) in species diversity, changes in species distributions, and losses of habitat types or ecosystem states (Holling 1973; Rapport et al. 1985; Steedman and Regier 1987). Li et al. (1987), Bisson et al. (1992), and Reeves et al. (1993) noted that native salmonid assemblages are simplified in watersheds that have been impacted by various human activities. Native nonsalmonids or introduced species often dominate fish communities in altered ecosystems (Li et al. 1987; Bisson et al. 1992). Habitat degradation is widespread across the region as a result of past and present activities (Bisson et al. 1992; McIntosh et al. 1994). Degradation of terrestrial ecosystems in the PNW (Thomas et al. 1993) and elsewhere (e.g., Wilcove et al. 1986; Rolstad 1991) has resulted in similar changes in terrestrial species assemblages.

Past and many present approaches to management of freshwater habitats of anadromous salmonids have focused on mitigating losses rather than preventing them. This strategy has generally not been successful (Bisson et al. 1992) and habitat loss and degradation continue. Williams et al. (1989) also found that such a strategy failed to halt the decline of habitat quantity and quality for other freshwater fishes. Naturally variable ocean conditions increase the importance of freshwater habitats to anadromous salmonids (Thomas et al. 1993). As a result of this dependence on freshwater habitats and the extensive amount of habitat degradation that has occurred, protection and restoration of upslope and fluvial processes that create and maintain habitats must be an integral component of any recovery program.

Habitat losses may result from human activities that directly destroy habitats or change the long-term dynamics of ecosystems (Rapport et al. 1985; Webb and Thomas 1994). Recent proposals for restoring and protecting habitats of at-risk fishes (e.g., Reeves and Sedell 1992; Thomas et al. 1993; Moyle and Yoshiyama 1994) addressed habitat destruction, primarily through the establishment of watershed-level reserves in which human impacts would be minimized, as advocated by Sheldon (1988) and Williams et al. (1989). We are not aware of anyone who has explicitly addressed long-term ecosystem dynamics in the context of fish conservation. Williams et al. (1989) called for recovery efforts to restore and conserve ecosystems rather than simply habitat attributes, but they did not state how to accomplish this. Williams et al. (1989) also noted that the failure to address this concern may be a major reason no fish species has ever been recovered after listing under the U.S. Endangered Species Act (ESA; 16 U.S.C. §§ 1531 to 1544).

The purpose of this paper is to examine components of strategies necessary to provide habitat for ESUs of anadromous salmonids in the PNW. Specifically, we will consider the role of natural disturbances in creating and maintaining habitats and how an understanding of this role might be incorporated into long-term recovery planning.

Ecosystem and Spatiotemporal Considerations

May (1994) noted that the most pressing challenge to conservation biology is the need to understand the responses of organisms over large temporal and spatial scales. Some relationships between habitat condition and individual salmonid response have been well established at the scales of habitat unit (e.g., Bisson et al. 1982; Nickelson et al. 1992), stream reach (e.g., Murphy et al. 1989), and (to a lesser extent) watershed (Schlosser 1991). But there is little understanding about how biological entities such as ESUs may respond to habitat patterns at large spatial scales. An initial hurdle in recovery planning for ESUs is identifying appropriate spatial and temporal scales on which to focus.

The ESA requires that ecosystems be considered in the development of recovery plans. The ESUs of anadromous salmonids generally encompass large geographic areas (e.g., Snake River basin in Idaho, upper Sacramento River and its tributaries in northern California). It is difficult to delineate the freshwater ecosystem of an ESU over such large areas. We believe that it is reasonable to consider the composite of individual watersheds within the geographic range of an ESU to be the "ecosystem" and to direct conservation and recovery efforts for freshwater habitats toward the populations that make up an ESU. Currens et al. (in press) suggest that appropriate temporal scales for populations are several decades to centuries and that spatial scales should begin at the watershed level (Figure 1). Although temporal considerations have not been addressed explicitly, recent proposals for restoring and conserving freshwater habitats of anadromous salmonids have emphasized watersheds (e.g., Reeves and Sedell 1992; Thomas et al. 1993; Moyle and Yoshiyama 1994). We concur with this direction and believe that for management and imple-

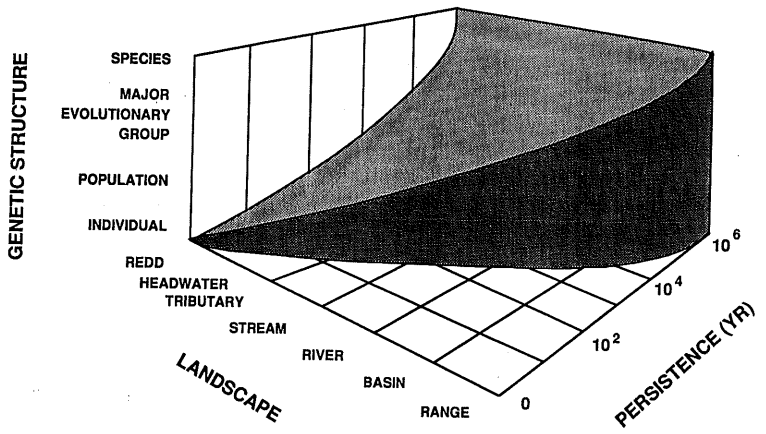

FIGURE 1.—A general hierarchial model of biological levels of organization for anadromous salmonids and the spatial and temporal scales that influence them (from Currens et al., in press).

mentation purposes, the individual watershed is the appropriate focus for recovery plans.

Within watersheds, recovery programs for ESUs must address not only root causes directly responsible for the immediate loss of habitat quantity and quality but also ecosystem processes that create and maintain habitats through time. In developing an ecosystem approach to the conservation and restoration of endangered organisms, it must be recognized that ecosystems are generally dynamic in space and time because of natural disturbances, particularly at large spaciotemporal scales (Botkin 1990).

A mosaic of conditions occurs within an ecosystem at any time as a consequence of disturbances (White and Pickett 1985). Any disturbed patch develops different habitat conditions or states over time. The assemblage of organisms in a particular patch changes with changing habitat conditions (Table 1; Huff and Raley 1991; Raphael 1991). Points along the trajectory of disturbance and recovery represent various states in the potential range of states that an ecosystem may exhibit. The locations of patches in particular states shift across the landscape due to the stochastic nature of most natural disturbances. In the PNW, terrestrial ecosystems are very dynamic in space and time as a result of natural disturbances such as fire and wind (Agee 1991, 1993). Holling (1973) noted that if resources are to be sustained, the dynamic nature of ecosystems and the need to maintain the diversity of ecosystem states must be recognized. Attempts to view and manage systems and resources in a static context may increase the rate of extinction of some organisms (Holling 1973).

Persistence in Dynamic Environments

It is unlikely that individual populations persist over long terms at the local scale in a dynamic environment (Hanski and Gilpin 1991; McCauley 1991; Mangel and Tier 1994). In dynamic environments, "... some patches are empty (but liable for colonization), while others are occupied (but liable to extinction). In such circumstances, the lights of individual patches wink on and off unpredictably, but the overall average level of illumination—the overall density of the metapopulation—may remain

TABLE 1.—Bird species found in different seral stages of Douglas-fir forests of Oregon and Washington (from Huff and Raley 1991).

Species	Seral stage		
	Early	Mid	Late
Chestnut-backed chickadee *Parus rufescens*	X	X	X
Hermit warbler *Dendroica occidentalis*	X	X	X
Western flycatcher *Empidonax difficilis*		X	X
Winter wren *Troglodytes troglodytes*		X	X
Red-breasted nuthatch *Sitta canadensis*	X		
Swainson's thrush *Catharus ustulatus*	X		
American robin *Turdus migratorius*	X		
Northern spotted owl *Strix occidentalis caurina*		X	
Pileated woodpecker *Dryocopus pileatus*		X	
Varied thrush *Ixoreus naevius*		X	

relatively steady" (May 1994). Metapopulations persist in dynamic environments through a suite of adaptations. Response to change varies with the level of biological organization (Karr and Freemark 1985; White and Pickett 1985). Physiological, morphological, and behavioral adaptations occur at the individual level. Life history patterns (Stearns 1977), reproductive rates, and modes of dispersal (Vrijenhoek 1985) are adaptations at the population level.

Several studies have documented the response of terrestrial populations to periodic catastrophic disturbances. Christensen (1985) cited examples of declines in small-mammal populations after fires in shrublands. Populations recovered after the vegetation did, and immigration from surrounding areas was a primary factor in the mammal recoveries. Colonizers of perturbed areas may be genetically predisposed to disperse (Sjorgen 1991) surplus to other populations (Hanski 1985; Pulliam 1988) or chance arrivals (Goodman 1987). Such adaptations increase the probability that metapopulations will persist through time.

The Dynamic Aquatic Environment

Aquatic ecologists and managers often do not have the long-term dynamic view of ecosystems held by terrestrial ecologists (White and Pickett 1985) and advocated by Holling (1973). Streams in the PNW (Resh et al. 1988) and elsewhere (Pringle et al. 1988; Reice 1994) are dynamic within relatively short time frames; typically a year to a decade, at the watershed scale, in response to floods or mass wasting (Swanston 1991). It is generally held that biological populations (some of them but not the entire assemblage) and physical features of these systems recover relatively quickly after such disturbances (e.g., Bisson et al. 1988; Lamberti et al. 1991; Pearson et al. 1992). Similar short-term responses of lotic fishes to disturbances have been noted in other areas (e.g., Hanson and Waters 1974; Matthews 1986). Over extended periods, habitat conditions in streams of similar size within a geomorphic region should be relatively uniform within and among watersheds (Vannote et al. 1980).

In contrast to terrestrial ecology, no theory predicts the mosaic of aquatic conditions or ecological states caused by disturbances and the corresponding responses of fish populations over extended periods. Minshall et al. (1989), Naiman et al. (1992), and Benda (1994) have proposed that aquatic ecosystems are dynamic in space and time at the watershed scale. The type, frequency, intensity and effect of disturbance vary with channel size and location within the watershed (Benda 1994).

An Oregon Example

The natural disturbance regime in the central Oregon Coast Range includes infrequent stand-resetting wildfires and frequent intense winter rainstorms. Wildfires reduce the soil-binding capacity of roots. When intense rainstorms saturate soils during periods of low root strength, concentrated landsliding into channels and debris flows may result. Such naturally occurring disturbances in stream channels can have both immediate impacts on and long-term implications for anadromous salmonids. Immediate impacts include direct mortality, habitat destruction, elimination of access to spawning and rearing sites, and temporary reduction or elimination of food resources. Longer-term effects may be positive, however; landslides and debris flows introduce essential habitat elements, such as large wood and sediment, into channels and affect storage of these materials. The configuration of channel networks, the delivery, storage, and transport of sediment and wood, and the decomposition of woody debris interact to create, maintain, and distribute fish habitat over the long term.

Three streams in the central Oregon Coast Range were examined to explore some of the responses of salmonids and their habitats to the natural disturbance regime (G. H. Reeves, U.S. Forest Service, Pacific Northwest Research Station, unpublished data). The streams have gradients between 1 and 2.5% and drainage areas between 14 and 18 km^2. Benda (1994) examined these and other streams as part of a study to model watershed erosion and sedimentation. Summer habitats and assemblages of juvenile anadromous salmonids were inventoried in 1988 and 1989. The time since catastrophic wildfire and hillslope failure differed among streams.

The watershed of Harvey Creek was burned by an intense wildfire in the late 1800s, and the forest was principally 90–100-year-old Douglas fir *Pseudotsuga menziesii* at the time of the study. The channel contained a large volume of sediment in storage throughout the lower portion of the drainage network and thus was considered to be in an aggradational state (mean depth of deposits, 1.8 m). Evidence of burned wood in the channel indicated widespread landsliding followed the fire. Gravel was the dominant substrate (Figure 2). Larger substrate particles and large woody debris were buried in the gravel deposits. Deep pools (mean depth, 0.9 m),

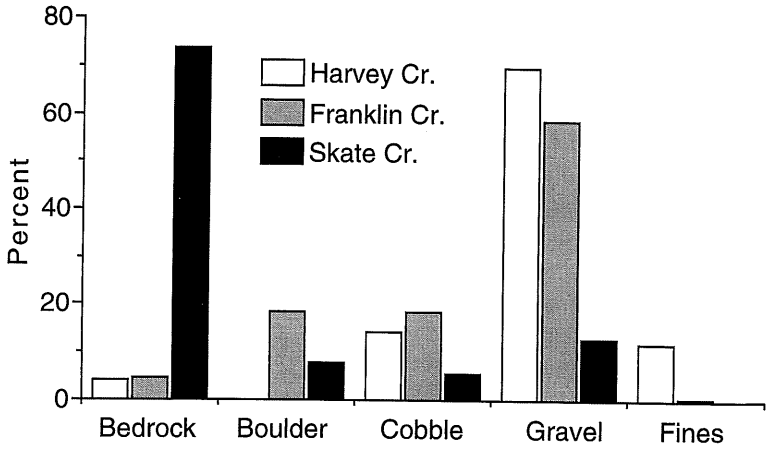

FIGURE 2.—Substrate composition in three streams of the central Oregon Coast Range that had differing histories of major natural disturbance. The time since the last major natural disturbance was 90–100 years for Harvey Creek, 160–180 years for Franklin Creek, and more than 330 years for Skate Creek. Cr = Creek (G. H. Reeves, unpublished data collected in July 1988 and 1989).

usually formed by scour around large wood, were the most common habitat units but were not hydraulically complex. Fewer pieces of large wood were observed in Harvey Creek than in the other study streams (Table 2), because wood deposited in the channel by the hillslope failure had been buried beneath sediment and little wood was being recruited from the relatively young surrounding forest. The juvenile salmonid assemblage was numerically dominated by age-0 coho salmon *Oncorhynchus kisutch*, but age-1 steelhead *O. mykiss* (about 1%) and cutthroat trout *O. clarki* (about 1%) were also present (Table 3).

The Skate Creek watershed was forested by trees more than 330 years of age, suggesting that the stream had not been subjected to a fire or hillslope failure for a long time. Habitat conditions in the stream were very simple. The substrate was predominantly bedrock and boulders with small, localized patches of stored sediment (Figure 2). Riffles were thin sheets of water flowing over bedrock. Although large wood was more abundant than in the other streams examined (Table 2), the lack of a deformable gravel bed greatly limited the wood's effectiveness in forming pools. Therefore, pools were shallow (mean depth, 0.1 m) and often in bedrock depressions. Juvenile coho salmon were the only salmonids found in Skate Creek (Table 3).

Franklin Creek was intermediate in time since disturbance. Based on the present vegetation, we estimated that catastrophic wildfire and landsliding occurred 160–180 years ago in this watershed. Mean depth of sediment in the channel was 0.7 m, and there was a greater array and more even distribution of substrate types than in the other streams (Figure 2). Mean pool depth was 0.35 m, less than half the mean depth of pools in Harvey Creek. As a result of sediment transport from the channel that

TABLE 2.—Mean number of pieces of large wood (>0.3 m in mean diameter and >3 m long) per 100 m in three streams of the central Oregon Coast Range that had differing histories of major natural disturbance (G. H. Reeves, unpublished data collected in July 1988 and 1989).

Stream	Years since last major disturbance	Mean pieces of wood/100 m
Harvey Creek	90–100	7.9
Franklin Creek	160–180	12.3
Skate Creek	>330	23.5

TABLE 3.—Composition of the assemblage of juvenile anadromous salmonids in three streams of the central Oregon Coast Range that had differing histories of major natural disturbance (G. H. Reeves, unpublished data collected in July 1988 and 1989).

Stream	Mean percent of estimated total numbers		
	Age-0 coho salmon	Age-1 steelhead	Age-1 cutthroat trout
Harvey Creek	98.0	1.0	1.0
Franklin Creek	85.0	12.5	2.3
Skate Creek	100.0	0.0	0.0

partially excavated buried wood and of recruitment of wood from the surrounding riparian forest, Franklin Creek had more pieces of large wood than Harvey Creek, though fewer than Skate Creek (Table 2). The combination of these factors produced the most complex habitat conditions observed in the three streams. Coho salmon numerically dominated the juvenile salmonid assemblage, but steelhead and cutthroat trout were relatively more abundant than in Harvey Creek (Table 3). Botkin et al. (1995) found that the healthiest stocks of various anadromous salmonids in coastal Oregon and northern California occurred where riparian vegetation within 0.5 km of the stream was similar to that found along Franklin Creek.

These field observations and a simulation model developed by Benda (1994) indicate that under the natural disturbance regime, variation in the timing and location of erosion-triggering fires and storms results in episodic delivery of materials that cause stream channels to alternate between aggraded and degraded sediment states. This generates spatial and temporal variability in both habitat conditions (Figure 3) and components of the juvenile salmonid assemblage within and among watersheds. Benda's (1994) simulation model indicated that wildfires of a mean size of about 30 km^2 occurred in the central Oregon Coast Range over the past 3,000 years with a return interval of 200–300 years. The cumulative probability of wildfire increased with increasing watershed size; for a 200-km^2 drainage basin, the frequency of stand-resetting wildfires was once every 45 years.

At a coarse level of resolution, Benda's (1994) model predicted that channels in watersheds of similar drainage area have characteristic patterns of sediment delivery, storage, and transport that vary with position in the drainage network and drainage area. Under a natural fire regime, for example, streams in the upper drainage experience large sediment deposits (>1 m thick) infrequently (once every hundreds of years) because sources of mass failure are few and sediment bedload transport rates are low. Channels in the central part of the network (drainage area, 30–50 km^2) have the highest probability of containing thick sediment deposits, partly due to relatively high cumulative probabilities of upstream mass wasting. These channels experience cycles of accumulation and flushing as sediment is transported in waves into and then out of them. Channels higher than sixth order with large drainage areas (>100 km^2), are governed by lateral migrations rather than by cycles of filling and emptying. Sediment waves moving from tributaries into larger channels mix at tributary junctions. Although sediment waves occur once in 5–10 years, they probably are inconspicuous (depth, < 0.2m). Habitat conditions in unbraided channels in the lowest portion of the network likely are more uniform than in higher elevation channels. It is important to note that the occurrence of a particular state will be affected by local circumstances that influence sediment retention, such as the amount of large wood in the channel, but these were not modeled by Benda (1994).

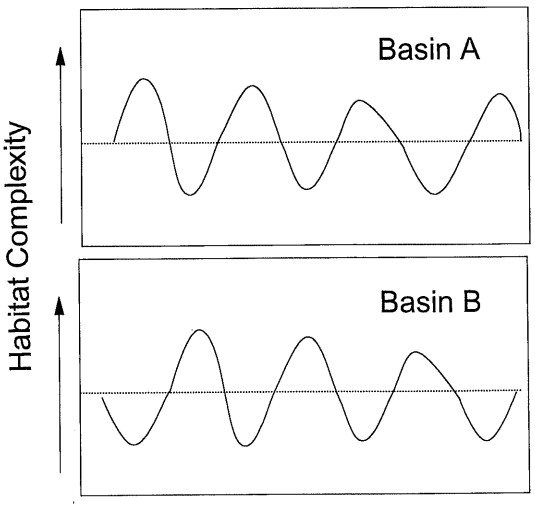

FIGURE 3.—Hypothetical historical conditions of fish habitat in different streams within and among watersheds in the central Oregon Coast Range (based on Benda 1994). The horizontal axis is time.

In the model, stream channels draining watersheds similar in area to Harvey, Franklin, and Skate creeks oscillated over time between states of sediment aggradation and degradation (Benda 1994). For central Oregon Coast Range channels, the average period between the state characterized by sediment deposits of intermediate depth, as exhibited in Franklin Creek, and the sediment-poor state was estimated to be more than 100 years. The model also produced an average duration of gravel-rich conditions of 80 years (range, 50–300 years) in small basins. Harvey Creek has apparently been gravel-rich for 100 years, and may continue to be so for another 100 years, although gravel-rich areas will likely move downstream over time. Again, the duration of a particular condition would be affected by local circumstances that were not modeled by Benda (1994).

Juvenile salmonid assemblages are likely associated with each state predicted by the model. Benda's (1994) simulation indicated that sediment supply would be limited at any given location in these small streams a majority of the time. Based on field observations, coho salmon would have dominated such simplified habitats. When a channel segment was not in this degraded state, it would shift between states of aggradation and intermediate sediment supply. Two additional salmonid species, steelhead and cutthroat trout, are expected to occur in aggraded channels. The intermediate state is characterized by intermediate sediment depths and more complex habitat, which should support a juvenile salmonid assemblage containing greater proportions of trout. Benda (1994) has developed long-term average probabilities for the time a channel segment would have spent in each state. Applied to a population of channels (those with similar gradient, drainage area, etc.) for a particular time, these probabilities can be used to estimate the landscape-scale mosaic of habitat conditions or biodiversity. For example, in watersheds of an area similar to those in the field example (approximately 25 km^2), the frequency distribution developed by Benda (1994) indicates that a majority of channel segments in the central Oregon Coast Range should have limited sediment supplies at any particular time and thus should contain relatively simple habitats.

A natural mosaic of habitat conditions for anadromous salmonids has likely existed elsewhere in the PNW; the features and relative proportion of each channel state should vary with climate, vegetation, drainage pattern, and spatial scale. Meyer et al. (1992) found cycles of aggradation and degradation associated with wildfires and hillslope failures in a Wyoming stream like those just described for the central Oregon Coast Range. It seems reasonable to assume that channel conditions over time were similar to those observed in the Oregon streams we examined.

In summary, the natural disturbance regime of the central Oregon Coast Range is described by the frequency, size, and spatial distribution of wildfires and landslides, and this regime has been responsible for developing a range of channel conditions within and among watersheds. The structure and composition of the juvenile anadromous salmonid assemblage varies with channel conditions. A disturbance regime that resembles this natural regime must be incorporated into any recovery plan for freshwater habitats of ESUs of anadromous salmonids.

Adaptations of Anadromous Salmonids

Anadromous salmonid populations in the Pacific Northwest are well adapted to dynamic environments. Adaptations include straying by adults, high fecundity, and mobility of juveniles. Straying by adults is genetically controlled, directly or indirectly (Quinn 1984), and aids the reestablishment of populations in disturbed areas on large (Neave 1958) and local scales (Ricker 1989). Strays would be reproductively most successful where local populations have been reduced or extirpated (Tallman and Healey 1994), provided there are suitable spawning and rearing conditions. Individuals from more than one population may recolonize depopulated areas, increasing the genetic diversity of the new population.

Movements of juveniles from natal streams to other areas also facilitate the establishment of new populations. Some individuals may be genetically programmed to move; others may be displaced from high-density populations (Northcote 1992). Chapman (1962) suggested that juvenile salmonids that were unable to obtain territories and migrated downstream were less fit individuals. However, at least some may leave voluntarily if emigration improves survival. Tschaplinski and Hartman (1983) found that juvenile coho salmon moving downstream in a small British Columbia stream took up residence in unoccupied habitats and grew rapidly.

High fecundity contributes to the establishment and growth of a local population if conditions are favorable. Pacific salmon are relatively fecund for benthic-spawning fishes with large eggs. Pink salmon *Oncorhynchus gorbuscha*, the smallest species, typically possess 1,200–1,900 eggs per female (Heard 1991). Adult female chinook salmon *O. tshawytscha*, the largest species, may contain more than 17,000 eggs (Healey 1991). Both high fecundity and large eggs contribute to the reproductive success of species whose young have extended periods of intragravel residence. These traits also facilitate growth when conditions are suitable.

Human Alterations of Disturbance Regimes

Natural ecosystems generally have a large capacity to absorb change without being dramatically altered. Resilience of an ecosystem is the degree to which the system can be disturbed and still return to a domain of behavior in which processes and interactions function as before (Holling 1973). If a disturbance exceeds the resilience of the system, the domain may shift and the system will develop new conditions or states that had not previously been

exhibited. Yount and Niemi (1990), modifying the disturbance definition of Bender et al. (1984), distinguished "pulse" disturbances from "press" disturbances. A pulse disturbance allows an ecosystem to remain within its normal bounds or domain and to recover the conditions that were present prior to disturbance. A press disturbance forces an ecosystem to a different domain or set of conditions. Yount and Niemi (1991) considered many anthropogenic disruptions, such as timber harvesting and urbanization, to be press disturbances. Gurtz and Wallace (1984) hypothesized that stream biota may not be able to recover from the effects of anthropogenic disturbances because these have no analogues in the natural disturbance regime, and organisms may not have evolved the appropriate breadth of habitat or reproductive requirements.

Modifications in the type of disturbance or in the frequency and magnitude of natural disturbances can alter the species composition, habitat features, and resilience of an ecosystem (White and Pickett 1985; Hobbs and Huenneke 1992). Alteration or loss of habitats as a result of changes in the disturbance regime can bring on extirpation of some species, increases in species favored by available habitats, and invasions of exotic organisms (Levin 1974; Harrison and Quinn 1989; Hansen and Urban 1992). We also believe that changes in the legacy of disturbance (the conditions that exist immediately following a disturbance) may be another important component of disturbance regimes that can be altered. Changes in the legacy can influence a system's resiliency by altering habitat conditions created immediately following a disturbance and by altering future conditions.

We do not mean to imply that every human action or activity causes a press disturbance; the impact of anthropogenic disruptions is minimal in some ecosystems (e.g., Attiwill 1994a, 1994b). However, we believe human activities that affect anadromous salmonids and their habitats, such as timber harvesting, urbanization, and agriculture, do generate press disturbances. These disturbances can result in the loss of habitats or ecosystem states necessary for various anadromous salmonids (Hicks et al. 1991; Bisson et al. 1992). Human activities in the PNW have altered the recovery potential of ecosystems, which may be as responsible for the decline of habitat as the direct impact of the activity itself.

A Disturbance-Based Ecosystem Approach to Freshwater Habitat Recovery

We believe that any long-term program for restoring and maintaining freshwater habitats for ESUs of anadromous salmonids must accommodate the dynamic nature of the PNW landscape. Given the dynamic nature of terrestrial ecosystems (Agee 1991, 1993), the links between terrestrial processes and aquatic ecosystems, the apparent adaptations of anadromous fish for persisting in a dynamic environment, and the limited available evidence (based on central Oregon Coast Range streams) of non-steady-state behavior of sedimentation and habitats, we believe a dynamic approach is advisable in any recovery program. In the following sections, we describe the components that should be included in this approach.

Watershed Scale Reserves: Short- and Long-term Considerations

Anadromous salmonids exhibit typical features of "patchy populations"; they exist in a dynamic environment and have good dispersal abilities (Harrison 1991, 1994). Conservation of patchy populations requires the conservation of numerous patches of suitable habitat and the potential for dispersal among them (Harrison 1991, 1994). Size and spacing of reserves should depend on the behavior and dispersal characteristics of the species of concern (Simberloff 1988). Rieman and McIntyre (1995) used logistic regression to investigate the influence of patch size, as well as stream width and gradient, on populations of bull trout *Salvelinus confluentus* at the reach, stream, and watershed scales. This approach could be helpful in identifying critical features of reserves for anadromous salmonids. In our current thinking on reserve planning for ESUs of anadromous salmonids, we consider patches to be watersheds, the size of which should depend on the species and geographic location. It is difficult to predict the exact number of patches required to sustain an organism (Lawton et al. 1994). Lande (1988) could do this for the northern spotted owl because data were available on essential life history variables. It is unlikely that predictions could be obtained for many other species, including ESUs of anadromous salmonids, because necessary life history data are often lacking (Lawton et al. 1994).

In the short term, reserves should be established in watersheds with good habitat conditions and functionally intact ecosystems to provide protection for these remaining areas. Reserves of this type are likely to be found in wildernesses and roadless areas on federal lands. Examples of watersheds that fulfill this requirement include some of the key watersheds identified by Reeves and Sedell (1992), the class I waters of Moyle and Yoshiyama (1994), and

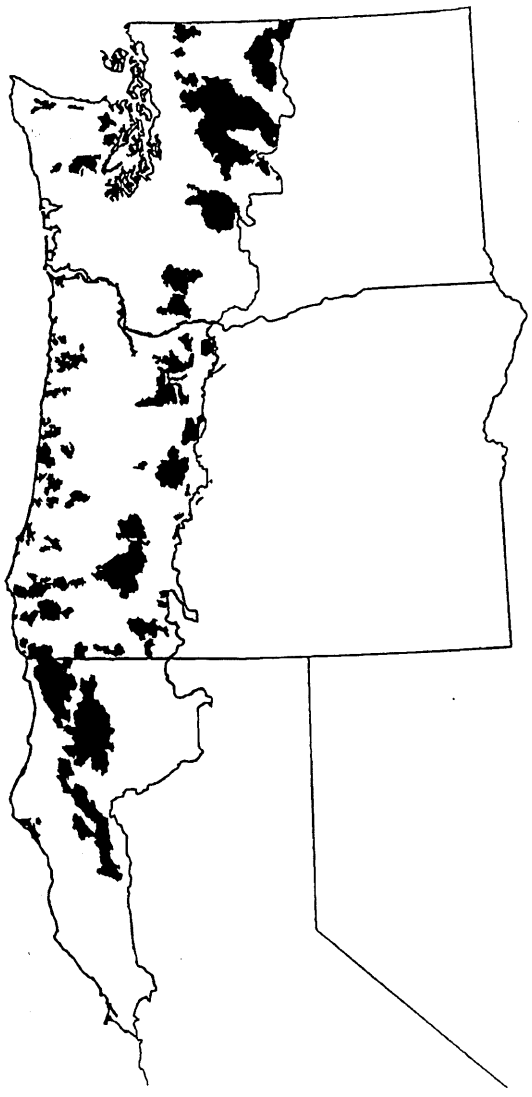

FIGURE 4.—Distribution of tier 1 key watersheds identified by Thomas et al. (1993).

the tier 1 key watersheds of Thomas et al. (1993) (Figure 4). Ideally these reserves should be distributed across the range of an ESU and should contain subpopulations of it. Because of the critical importance of these watersheds in the short term, activities within them should be minimized or modified to protect the integrity of existing physical and ecological conditions.

Identification of watersheds that have the best potential for being restored should also be a short-term priority of any recovery strategy. These watersheds could serve as the next generation of reserves. Systems should qualify based on the extent of habitat degradation and the degree to which their natural diversity and ecological processes are retained. Examples of such watersheds are some of the key watersheds identified by Reeves and Sedell (1992), some tier 1 key watersheds identified by Thomas et al. (1993), the class III waters of Moyle and Sato (1991), and the class III waters of Moyle and Yoshiyama's (1994) aquatic diversity management areas. Restoration programs implemented in these watersheds should be holistic in their approach. They should address instream habitat concerns, prevent further degradation, and restore ecological processes that create and maintain instream habitats.

It is imperative to recognize and acknowledge that identified reserves will experience natural and, often, anthropogenic disturbances. Thus, simply putting aside a fixed set of watersheds as reserves may not provide habitats of sufficient quantity and quality to ensure long-term persistence of ESUs. Conservation reserves have generally been established and managed without consideration of long-term disturbance dynamics and the biological and evolutionary processes that influence organisms contained within them (Western 1989). Consequently, their populations may have higher probabilities of extirpation in the long term than expected. Reasons for this include isolation of reserves from surrounding areas of suitable habitat resulting from habitat fragmentation (MacArthur and Wilson 1967; Diamond and May 1976); restriction or elimination of migration and dispersal (Elsenberg and Harris 1989; Harris and Elsenberg 1989); and boundary effects associated with surrounding areas, such as invasion of native and exotic competitors, disease, and pollution (Shonewald-Cox 1983; Wilcox 1990). Hales (1989) and White and Bratton (1980) noted that in dynamic landscapes, reserves may act as holding islands that persist only for relatively short ecological periods (100–200 years). Reserves should be large enough to allow operation of the natural disturbance regime and to support a mosaic of patches with different biological and physical attributes (Pickett and Thompson 1978).

Gotelli (1991) noted that reserve strategies such as those proposed by Harrison (1991, 1994) do not address the longevity of patches. This is a major concern in dynamic environments like those of the PNW. Modification of the strategy proposed by Harrison (1991, 1994) to accommodate a dynamic environment is a prudent approach in the development of a recovery strategy for anadromous salmo-

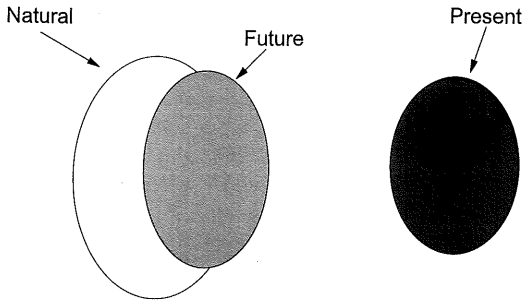

FIGURE 5.—Conceptual representation of the range of conditions experienced by aquatic ecosystems historically, currently, and under a new disturbance regime (modified from H. Regier, University of Toronto, personal communication).

nid habitats. Specifically, there is need for a shifting mosaic of reserves that change location in response to the ability of specific watersheds to provide suitable habitat conditions.

A New Human-Influenced Disturbance Regime

Under natural wildfire regimes of the PNW, the condition of freshwater habitats for anadromous salmonids was likely regulated by episodic delivery of sediment and wood to the channel. Given that human demands on ecosystems will only increase, we believe that returning the entire landscape to the natural wildfire regime will not be possible. Therefore, human activities will have to be molded into an analogous disturbance regime if habitats are to recover and persist. First must come an understanding of how the natural disturbance regime created and maintained habitats for anadromous salmonids through time and how it has been modified by human activity. Then it will be necessary to identify those human activities that can be altered to maintain desired ecological processes and leave the legacy that allows recovery and persistence of required freshwater habitats. In other words, the character of anthropogenic disruption must be shifted from a press to a pulse disturbance (Yount and Niemi 1990) (Figure 5). The following is an example of how we believe timber harvest and associated activities, as currently practiced on federal lands in the central Oregon Coast Range, have affected habitat and biodiversity of anadromous salmonids and how these could be adjusted to help create suitable conditions in space and time. We believe that timber management may offer more immediate opportunities than agricultural or urban processes for modifying practices to create a human-influenced disturbance regime that maintains components of the natural regime.

Disturbance caused by timber harvest differs from stand-resetting wildfires in the central Oregon Coast Range in several respects. One difference is the legacy of the disturbance. Wildfires left large amounts of standing and downed wood (Agee 1991), which was often delivered to channels along with sediment in storm-generated landslides (Benda 1994). This promoted development of high-quality habitats as sediment was transported from the system, leaving the wood behind (Benda 1994). Timber harvest, as it is generally practiced, reduces the amount of large wood available to streams (Hicks et al. 1991; Reeves et al. 1993; Ralph et al. 1994), so when harvest-related hillslope failures occur, sediment is the primary material delivered to the channel (Hicks et al. 1991). Because large wood is an integral component of aquatic habitats and a major influence on sediment transport and storage, the potential for developing complex habitats is much lower when small rather than large amounts of wood are in the channel. Consequently, channels may be simpler following timber harvest than they are after wildfires.

The interval between events also affects the conditions that develop after a disturbance (Hobbs and Huenneke 1992). Under the natural disturbance regime, variation in the timing and location of erosion-triggering fires and storms probably caused stream channels to alternate between aggraded and degraded sediment states, generating temporal variability in both fish habitats and assemblages of juvenile salmonids. Wildfires occurred on average about once every 300 years in the central Oregon Coast Range (Benda 1994). In watersheds smaller than 30 km^2, postfire development of the most diverse physical and biological stream conditions may have taken 150 years or more (see earlier discussion). Timber harvest generally occurs at intervals of 60–80 years on public lands and 40–50 years on private timberlands. This may not allow sufficient time for the development of conditions necessary to support the array of fishes found under natural disturbance regimes.

A third difference between timber harvest and a disturbance regime dominated by wildfire is the spatial distribution of each. Based on a fire frequency of once every 300 years, Benda (1994) estimated that on average, 15–25% of the forest in the central Oregon Coast Range would have been in early successional stages because of recent wildfires. In contrast, the area affected by timber harvest is

much greater. For example, in the Mapleton District of the Siuslaw National Forest, which contains the watersheds studied by Benda (1994), approximately 35% of the forest is in early succession (J. Martin, Siuslaw National Forest, personal communication). If private lands were included, the percentage would be greater. The present forested landscape is more homogeneous with respect to seral stage than it was historically. Just as the distribution of terrestrial habitat has been altered by switching from a wildfire-driven to a harvest-driven disturbance regime, it is also possible that the distribution of aquatic habitats is different today than it was under the natural disturbance regime and thus less capable of supporting a diverse juvenile salmonid assemblage.

A fourth difference between the natural wildfire-driven and the current harvest-driven regime is the size of disturbance and the landscape pattern generated by the disturbance. Timber on federal lands has typically been managed by widely dispersed activities; approximately 174,000 km of roads exist across public lands in the range of the northern spotted owl (Thomas et al. 1993), and many millions of hectares have been affected by small harvests of approximately 16 ha. Wildfires, on the other hand, often generate a larger but more concentrated disturbance. When wildfires occurred in the central Oregon Coast Range, they tended to be large (mean, 3,000 ha), stand-resetting fires (Benda 1994). Consequently, the spatial pattern and amount of sediment delivered to channels would likely be different under these two disturbance regimes. In naturally burned areas, storms occurring during periods of low root strength would generate large volumes of sediment from nearly synchronous hillslope failures and channels would become aggraded. Subsequently, delivery would be reduced while source areas recharged. This, coupled with downstream flushing of stored sediments, would bring the channel to an intermediate level of sediment storage and a corresponding period of high-quality habitat. In unburned watersheds, sediment delivery rates would remain low. In contrast, timber harvest activities are dispersed; thus, we presume that mass wasting would be more widely distributed and would deliver sediment at elevated rates in most managed watersheds. Storm-generated landslides would be asynchronous, being governed through time by harvest schedules. Cycles of channel aggradation and degradation probably would not be apparent and sediment delivery, at a landscape scale, would likely be chronic rather than episodic. These factors would conspire to produce relatively low-quality habitats across the landscape and eliminate the potential for attaining the most complex habitat states.

In summary, the differences between present timber harvest disturbance regime and the natural disturbance regime have important implications for stream ecosystems and anadromous salmonids. Stream habitat, at a point in the channel, is less complex under the timber harvest regime (Hicks et al. 1991; Bisson et al. 1992) than under the natural regime, and the potential for achieving greater complexity is also reduced. This is primarily a result of the reduced legacy and shorter interval between disturbance events under the timber harvest regime. In addition, landscape-level habitat heterogeneity is reduced under the harvest regime because the disturbance is more dispersed and widespread.

The new disturbance regime created by timber harvest should address the concerns just listed. The legacy of hillslope failures associated with timber management activities needs to include more large wood. Benda (1990) identified the attributes of first- and second-order streams that favor the delivery of desirable material to fish-bearing channels. Increasing the extent of riparian protection along these streams, as proposed by Thomas et al. (1993), obviously increases the potential delivery of wood. Such a strategy may not result in wood loadings as large as occurred naturally because trees away from the riparian zone will have been removed. However, this strategy should increase wood loadings beyond what is currently possible and should allow channels to develop more complex habitats.

Longer intervals between harvest rotations could be another component of this new disturbance regime. In single basins in the central Oregon Coast Range, the desirable interval may be 150–200 years, although this is a first approximation. The exact interval would depend on the magnitude and areal extent of the natural disturbance regime and the time it takes for favorable habitat conditions to develop if adequate large wood and sediment are available. It will be different in other regions. Extending rotation time would also provide benefits to many terrestrial organisms.

Concentrating rather than dispersing management activities could be another element of the new disturbance regime. This would more closely resemble the pattern generated by natural disturbances than does the current practice of dispersing activity in small areas. For example, if a basin has four subwatersheds, it may be better to concentrate activities in one for an extended period (50–75 years) than to operate in 25% of each one at any time

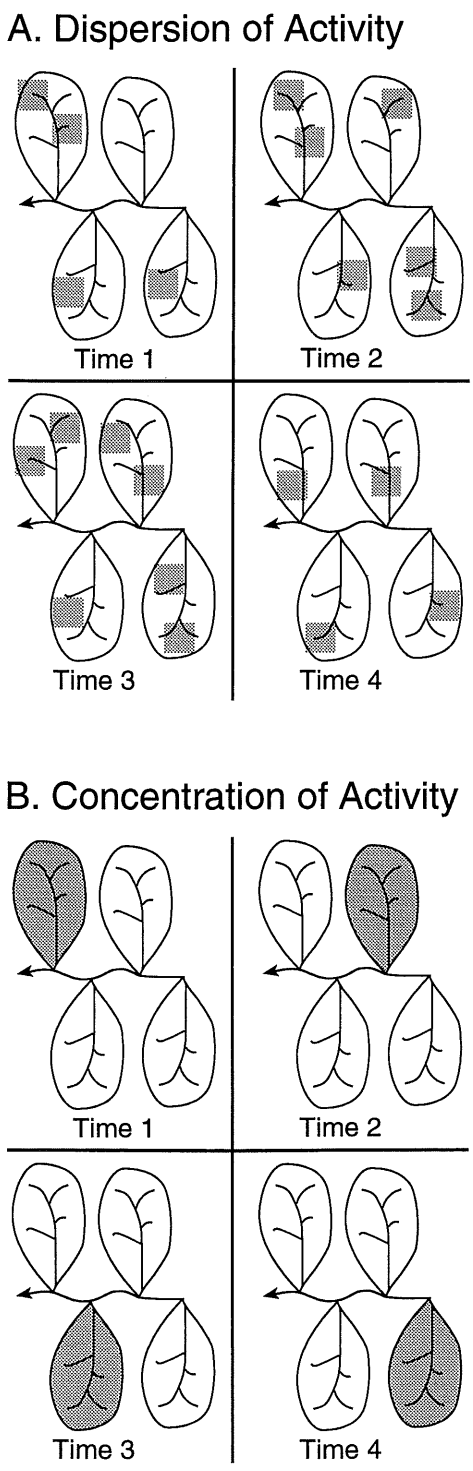

FIGURE 6.—Examples of patterns resulting from (**A**) dispersing and (**B**) concentrating land management activities in a watershed over time (modified from Grant 1990).

(Figure 6). Grant (1990) modeled such a scenario to determine its effects on patterns of peak flow and found that there was little difference between the two approaches. Franklin and Forman (1987) believed that dispersing activity (Figure 6A) increases habitat and landscape fragmentation and is more detrimental than concentrating activities (Figure 6B) to terrestrial organisms that require late-successional forests. We believe that concentrating activity would have similar benefits for the aquatic biota if the elements discussed previously are included. This approach could also be linked to planning future reserves and reducing risks in reserves, so it merits consideration in the development of habitat recovery efforts.

All of the elements discussed above must be included in the development of a new disturbance regime if the regime is to be successful at creating and maintaining habitats for anadromous salmonids. Exclusion of any element greatly reduces the potential for success. Our concept of designing a disturbance regime around human activities could complement parts of other strategies proposed for management of the central Oregon Coast Range (Noss 1993) and other parts of the PNW (e.g., Thomas et al. 1993). These call for reserves in which human activity is curtailed or eliminated. The proposed new disturbance regime could be applied to areas outside any such reserve system, particularly in the short term. It could also guide management strategies in reserves where limited human activity is allowed. The long-term goal of this effort would be to create refugia to replace and complement refugia in permanently designated reserves, such as wilderness areas and other withdrawn lands.

Conclusions

Plans directed at the freshwater habitat for ESUs of anadromous salmonids in the Pacific Northwest must be focused on restoring and maintaining ecosystem processes that create and maintain habitats through time. It is important to insure that as good habitats "wink out," either through anthropogenic or natural disturbances or through development into new ecological states, others "wink on." Designating the most intact remaining aquatic ecosystems as reserves is essential for meeting near-term requirements. In the long term, a static reserve system alone is unlikely to meet the requirements of these fish. Management must also be directed at developing the next generation of reserves. Strategies should be designed and implemented that treat land management activities as disturbance events to

be manipulated so as to retain the ecological processes necessary to create and maintain freshwater habitat through time. Although necessary for anadromous salmonids, the approach of moving reserves and managing periodic disturbances may not be suitable for locally endemic or immobile biota. It is imperative to consider the needs of other organisms in the development of any habitat recovery program for ESUs of anadromous salmonids.

Many hurdles must be overcome to make our approach effective. First, biologists, managers, and planners need to think in longer time frames than they are generally accustomed to using. They need to acknowledge that ecosystems are dynamic in space and time over these longer periods. Simply designating reserves and expecting these to function as such for extended periods may be unrealistic; some benefits may accrue in the short term, but in the long run it is unlikely that habitats of sufficient quality and quantity will be available to sustain ESUs of anadromous salmonids. Expectations about habitat conditions in streams must change; a stream will not always have suitable habitats for anadromous salmonids, and all streams should not be expected to have suitable habitats at the same time. A consequence of a dynamic view is that, perspectives must be regional (Holling 1973). The percentage of the landscape that should contain suitable habitats must be identified and the temporal and spatial distributions of these habitats determined.

Finally, disturbance must be recognized as an integral component of any long-term strategy. This will be a difficult hurdle to overcome. It requires educating resource managers, scientists, administrators, politicians, and the public so they realize that periodic disturbance is not necessarily negative. To the contrary, disturbance may be necessary in order to have productive habitats for ESUs of anadromous salmonids in the PNW over long periods.

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