

# 9

## Fish Communities

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### Overview

- Biological communities are best understood in terms of community dynamics and functional organization because of the difficulty in delineating communities as well-defined units. The structure and composition of fish communities in Pacific coastal stream systems vary with spatial scale from watershed to habitat units. The relative influence of biotic and abiotic factors has been the subject of much debate but generally varies according to spatial scale.

- Compared to other parts of North America, stream fish communities in the Pacific coastal ecoregion are relatively depauperate. A major reason for this is the large influence of geologic history, primarily extensive tectonic activity and glaciation. Although the species richness of the region is low, there is great diversity in life history and morphological types within and among populations.

- At the watershed scale, species richness generally increases downstream. This pattern follows the species-area relationship. Species gradually disappear and additional ones appear (are added) along the stream network. Physical factors strongly influence community structure and composition in headwater areas, whereas, biological factors are more important in lower portions of the watershed.

- At the reach scale, fish communities are generally more diverse in unconstrained reaches than in constrained reaches. These differences are attributable to differences in pro-

ductivity and habitat diversity between reach types.

- Biological factors and habitat complexity are major influences on fish communities at the habitat unit level. Generally the more diverse the habitat unit, the greater the community diversity. The influence of biotic factors, primarily competition, varies with the species present in the habitat. In some situations, competition for space or food restricts species presence. In other cases, partitioning of habitat and food resources allows more species to inhabit a particular unit.

- The diversity of stream fish communities throughout much of the Pacific coastal ecoregion has declined as a result of human activities. The general pattern of response is changes in relative abundance rather than loss of species. Some species respond positively while others decline in abundance.

- Integration of macroscale physical and biological processes into a broader spatial and temporal framework assists in understanding the dynamics of stream fish communities as well as recovering and maintaining native stream fish communities in the Pacific coastal ecoregion.

### Introduction

Ecological communities are currently viewed as dynamic entities whose members vary in space and time. A community consists of coadapted species with similar geographic distributions,



but most species are not in obligatory associations with each other because populations of species tend to change along environmental gradients (Whittaker 1962). Consequently, it is difficult to identify communities as well-defined units. Thus, community ecology now emphasizes the dynamics and functional organization of communities rather than the classification of communities into discrete units or types (Underwood 1986, Krebs 1994).

The organization of natural communities is influenced by environmental factors and biotic interactions (Sousa 1984, Schlosser 1987, Menge and Olson 1990, Rosenzweig 1994). Factors such as habitat heterogeneity, frequency and magnitude of physical disturbance, and life history attributes of organisms influence the structure and composition of communities, with the relative importance of physical and biological processes generally changing along environmental gradients (Connell 1975 and 1978, Karr and Freemark 1983 and 1985, Wiens 1984). Community composition is also influenced by historical processes, such as speciation and dispersal (Holt 1993).

The relative influence of physical and biological factors on the structure and composition of stream fish communities has been the subject of much debate. The "stochastic school" maintains that physical and temporal factors are dominant influences (Grossman et al. 1982). This view argues that species abundance varies and is largely determined by differential responses to unpredictable environmental changes. In contrast, the "deterministic" school argues that interactive biological mechanisms, such as competition and predation, are the primary determinants of community structure and composition (Yant et al. 1984). Power and Matthews (1983), Moyle and Vondracek (1985), and Schlosser and Ebel (1989) cite examples of streams in different part of the United States where biological interactions exert a strong influence on fish communities. Schoener (1987) noted that, as a group, stream fishes are unusual in the extent to which communities are influenced by both physical and biological factors. Schlosser (1987) argues that, at least for fish communities in small warmwater streams, the relative importance of

physical and biological processes varies with location within the stream network.

The ecology of many salmonid fishes in the Pacific coastal ecoregion has been studied extensively but relatively little is known about nonsalmonids or the organization of stream fish communities. Several studies have examined interactions between species, again primarily salmonids (Hartman 1965, Everest and Chapman 1972, Bisson et al. 1988). Li et al. (1987) reviewed factors influencing communities of stream fish in the Pacific Northwest, which includes the Pacific coastal ecoregion, but could not reach firm conclusions about how the communities were structured. One reason for this is that factors influencing the structure and composition of stream fish communities vary with spatial scale (Table 9.1). This chapter examines the structure and composition of fish communities at different spatial scales—regional, watershed, reach and habitat unit. For an explanation of terms and a general review of the concept of biodiversity, see Chapter 17.

## Regional Diversity

Relative to other areas of North America, the Pacific Northwest (including the Pacific coastal ecoregion) has comparatively fewer species of fish. The western United States has about one half of the families and one quarter of the fish species found in the eastern United States (Smith 1981, Minckley et al. 1986). Mahon (1984) estimated that in western areas there are 5 to 10 native fish species in a 10,000 km<sup>2</sup> watershed compared to 50 species in a similar sized watershed in Ontario, Canada.

Geological history has been a major influence on the fish fauna of the Pacific coastal ecoregion (Miller 1959). The ecoregion and surrounding areas have been more extensively affected by tectonic activity and glaciation than other areas of North America (McPhail and Lindsey 1986, Minckley et al. 1986). During the last glacial period, ice sheets covered much of Alaska, British Columbia, and northern Washington reaching their maximum extent about 15,000 years ago (Figure 9.1).

TABLE 9.1. Hierarchical organization of factors regulating fish species diversity in Pacific coastal streams.

Hierarchical level	Spatial scale (km <sup>2</sup> )	Physical events and processes	Biological events and processes	Environmental gradients
Region	10 <sup>8</sup> -10 <sup>6</sup>	Tectonism, volcanism, glaciation, sea level fluctuations	Invasion of oceanic taxa, speciation	Ocean/freshwater productivity, aridity, temperature
Basin	10 <sup>5</sup> -10 <sup>3</sup>	Stream capture, formation of falls, climatic change	Dispersion and isolation, subspecific endemism, stock differentiation, range expansion and contraction	Elevation, stream order/size, temperature
Reach	10 <sup>2</sup> -10 <sup>0</sup>	Alluvial/colluvial valley formation, fluvial disturbance	Species refugia and recolonization	Stream gradient, constraint, habitat diversity, productivity
Habitat unit	10 <sup>-1</sup> -10 <sup>-4</sup>	Sediment and organic debris storage and transport	Competition, predation	Habitat diversity, complexity

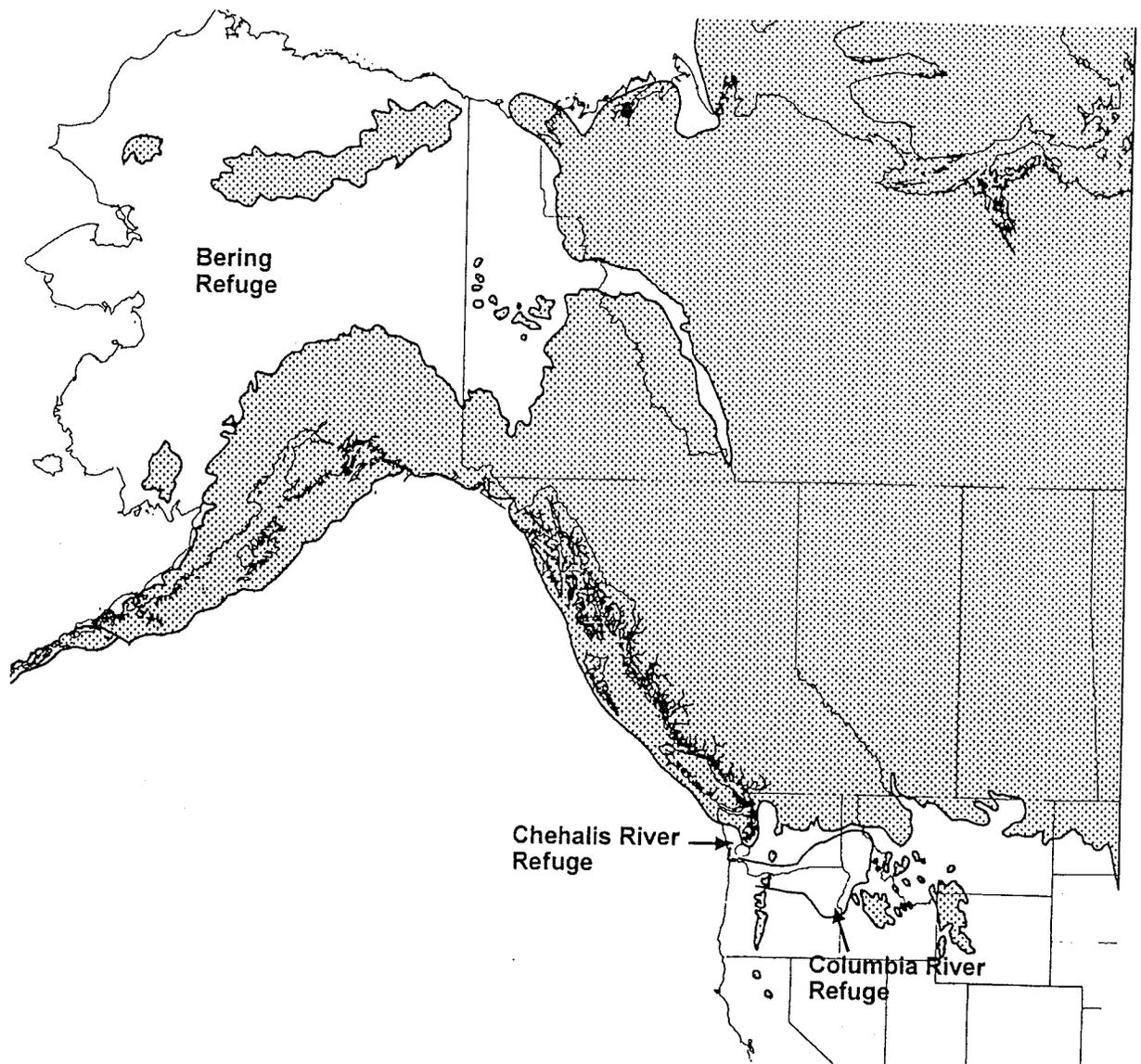


FIGURE 9.1. Distribution of glaciers in the Pacific Coastal Ecoregion during the last Ice Age.

Continental glaciers reached south into western Washington near what is now the southern tip of Puget Sound and along the Cascade Mountain Range into Oregon. At this time, three major refugia for fishes were present: the Bering refuge to the north, and refugia in the Chehalis and Columbia River basins in Washington (McPhail and Lindsey 1986). As the glaciers gradually retreated these three areas served as major sources of colonists for drainages in northern Washington and British Columbia. However, the relatively short duration of postglacial colonization (about 10,000 years) has contributed to a paucity of species in northern portions of the Pacific coastal ecoregion (McPhail and Lindsey 1986). The ability of many closely related species or stocks to hybridize when brought together (Behnke 1992, Smith et al. 1995) suggests that the relatively short time period following the last glaciation has been insufficient for evolutionary processes to produce a native fauna that rivals in species richness the much more diverse faunas of eastern United States and other parts of the world.

Modern fishes of the Pacific coastal ecoregion have been influenced by tectonic activities such as earthquakes, volcanism, and uplift resulting from the collision of continental plates. Primarily these activities separate formerly continuous habitats or join formerly isolated ones (Minckley et al. 1986). Changes in local conditions caused by tectonic activity, such as formation of mountains, alter environmental conditions and thus influence species abundance and distribution.

The history and specific effects of tectonic activity on fishes in the Pacific coastal ecoregion is too complex to present in detail. Suffice it to say, tectonic activity is responsible for the large number of endemic (i.e., species with local distributions) and the limited number of species in some river systems (Minckley et al. 1986). For example, the Klamath River in southern Oregon consists of discrete upper and lower areas that are separated by Klamath Falls. The upper area, historically connected to the Sacramento River system (California), was isolated from the Sacramento River in the late Miocene period (i.e., about 10 million years ago) after tectonic activity. However, the two systems

share common species that are not found in the lower Klamath River (Minckley et al. 1986). Fishes in the lower river resemble those in the Rogue River and other coastal systems. Another example of the effect of tectonic activities is seen in coastal Oregon streams. Much of coastal Oregon was under water in the Paleocene (i.e., 54–65 million years ago). Many streams, particularly smaller ones, had no connection with interior systems. Limited reinvasion of these systems by marine-tolerant species, such as salmonids (*Salmonidae*), lampreys (*Petromyzontidae*) and sculpins (*Cottidae*) occurred after ocean levels receded. Minckley et al. (1986) and McPhail and Lindsey (1986) provide descriptions on this topic.

As a group, fish in the Pacific coastal ecoregion and western North America have different morphologies and life histories compared to species from eastern North America (Table 9.2). A greater proportion of the fauna in the Pacific coastal ecoregion and western North America are larger (>30cm standard length [SL]), longer lived, older at age of first reproduction, and have longer reproduction spans and higher absolute fecundity than the fauna from eastern North America (Miller 1959, Moyle 1976). For example, in two major Pacific coastal ecoregion river systems (the Klamath and Columbia) large fishes represent 64% and 41% of the fauna, respectively (Moyle and Herbold 1987). Small fishes comprise 29% and 22% of the fauna, respectively. The fish fauna of eastern North America is dominated by smaller (<10cm SL), early reproducing fishes (Mahon 1984). In two eastern rivers, large fish represent 18% and 27% and small fish 41% and 55% of the fauna (Moyle and Herbold 1987).

Body size and life history features are adaptations to regional environmental conditions. Smaller size and earlier age at first reproduction is advantageous in environments where conditions may be more stable and adult survivorship is variable but reproductive success is high (Miller 1979, Mann et al. 1984). Larger body size, delayed age at first reproduction, and high relative fecundity and adult survivorship (but low reproductive success in any given year) are advantageous traits in

TABLE 9.2. General characteristics of fish faunas of the Mississippi River drainage and western North America.

Characteristic	Mississippi drainage	Western North America
Species richness		
Sample richness	High (10–30 species)	Low (<10)
Cumulative richness	High; increases rapidly in small streams, then levels out	Low; increases as stream size increases
Life history		
Bionomics	Short lives, early maturation, low fecundity, predominately short reproductive spans	Long lives (2+ years), late maturation, high fecundity, predominately long reproduction spans
Parental care	Brood hiders and guarders	Little parental care
Migration	Limited movements for most species; spawning migrations for some large species	Spawning migrations common, but occurrence variable
Trophic specialization	Relatively unspecialized invertebrate feeders common	Specialists common

Modified from Moyle and Herbold 1987 © University of Oklahoma Press.

variable environments (Moyle and Herbold 1987).

The freshwater fish fauna of the Pacific Northwest is dominated by lampreys, salmon, trout and chars (both anadromous and nonanadromous), minnows such as shiners, dace, chubs, and squawfish (Cyprinidae), suckers (Catostomidae), and sculpins. Stickleback (Gasterosteidae) are also common in many systems. Species richness is much greater in southern portions of the Pacific coastal ecoregion (i.e., Oregon and northern California), which were not glaciated during the last major glacial period. Fish communities in river basins in the northern portions are dominated by euryhaline (i.e., salt tolerant) species capable of dispersal through salt water. Endemism is fairly common in many of the isolated drainages of this area (Smith 1981, Minckley et al. 1986), particularly among lampreys, salmonids, cyprinids, and cottids (Moyle and Herbold 1987). In the Columbia Zoogeographic Province, 58% of the native fishes are endemic, while 37% of the fishes of the Klamath Zoogeographic Province (California and Oregon) are endemic (Moyle and Cech 1982). Most species with widespread distributions are capable of dispersal through the ocean or through fluvial connections between river basins (Miller 1959). Stream capture (action of a river acquiring a headwater of

a second river as a result of differential erosion rates between the two systems, or a change in landscape features resulting from tectonic activity) facilitates dispersal for species dwelling in adjacent headwaters (Bond 1963, Smith 1981).

Despite this paucity of species, native fishes are integral components of, and exert strong influences on, all trophic levels of ecosystems in the Pacific coastal ecoregion (Willson and Halupka 1995). Both terrestrial and aquatic larger animals occupying several trophic levels, (e.g., raccoons, dippers, deer and grizzly bears) use anadromous salmonids (*Oncorhynchus* spp.) as food sources during some part of the year in streams throughout the Pacific coastal ecoregion (Cederholm et al. 1989, Willson and Halupka 1995) (Table 9.3). Returning adults also provide nutrients for a suite of trophic levels (Bilby et al. 1996). Salmonid-derived nutrients,  $^{15}\text{N}$  and  $^{13}\text{C}$ , are incorporated into stream biota by consumption of eggs, carcasses, and fry, and sorption onto dissolved organic matter released by decomposing carcasses. Juvenile salmonids in streams with larger returning adult runs experience faster growth rates than do juveniles in streams with smaller runs. Decomposing carcasses also provide important sources of nitrogen for riparian vegetation. Additionally, because of predictable migra-

TABLE 9.3. Mammals and birds known to consume salmon carcasses in the Pacific coastal ecosystem.

Mammals	Birds
Beaver ( <i>Castor canadensis</i> )	Bald eagle ( <i>Haliaeetus leucocephalus</i> )
Black bear ( <i>Ursus americanus</i> )	Chickadees ( <i>Parus</i> spp.)
Blacktail deer ( <i>Odocoileus hemionus</i> )	Crow ( <i>Corvus</i> spp.)
Bobcat ( <i>Lynx rufus</i> )	Dipper ( <i>Cinclus mexicanus</i> )
Cougar ( <i>Felis concolor</i> )	Fox sparrow ( <i>Passerella iliaca</i> )
Coyote ( <i>Canis Latrans</i> )	Gray jay ( <i>Perisoreus canadensis</i> )
Deer mouse ( <i>Peromyscus maniculatus</i> )	Gulls ( <i>Larus</i> spp.)
Douglas squirrel ( <i>Tamiasciurus douglasii</i> )	Hairy woodpecker ( <i>Picoides villosus</i> )
Elk ( <i>Cervus elaphus</i> )	Hermit thrush ( <i>Catharus guttatus</i> )
Flying squirrel ( <i>Glaucomys sabrinus</i> )	Kingfisher ( <i>Megaceryle alcyon</i> )
Grizzly bear ( <i>U. arctos</i> )	Kinglets ( <i>Regulus</i> spp.)
Masked shrew ( <i>S. cinereus</i> )	Merlin ( <i>Falco columbarius</i> )
Mink ( <i>M. vison</i> )	Nuthatches ( <i>Sitta</i> spp.)
Mole ( <i>Scapanus</i> spp.)	Pine siskin ( <i>Carduelis pinus</i> )
Mountain beaver ( <i>Aplodontia rufa</i> )	Pygmy owl ( <i>Glaucidium gnoma</i> )
Otter ( <i>Lutra canadensis</i> )	Raven ( <i>C. corax</i> )
Raccoon ( <i>Procyon lotor</i> )	Red-tailed hawk ( <i>Buteo jamaicensis</i> )
Skunk ( <i>Mephitis mephitis</i> )	Robin ( <i>Turdus migratorius</i> )
Wandering shrew ( <i>S. vagrans</i> )	Ruffed grouse ( <i>Bonasa umbellus</i> )
Water shrew ( <i>Sorex palustris</i> )	Sapsucker ( <i>Sphyrapicus varius</i> )
Weasel ( <i>Mustela</i> spp.)	Song sparrow ( <i>Melospiza melodia</i> )
	Stellers jay ( <i>Cyanocitta stelleri</i> )
	Varied thrush ( <i>Ixoreus naevius</i> )
	Winter wren ( <i>Troglodytes troglodytes</i> )

From Cederholm et al. 1989, Willson and Halupka 1995.

tions, high food quality, and high commercial, recreational, and aesthetic value, many species are important components of human cultural, social, and economic systems throughout the region (Stouder et al. 1996).

### Anadromous Life Histories

Anadromous fishes comprise approximately 25% of the freshwater fishes in many river systems of the Pacific coastal ecoregion. Anadromous species begin life in freshwater, move to the marine environment to grow and mature, and then return to freshwater to reproduce. Species with anadromous life histories include some lampreys, sturgeons (*Acipenser transmontanus*, *A. medirostris*), salmon and trout, and candlefish (*Thaleichthys pacificus*). The predominance of fish with anadromous life histories increases from the equator to the poles in the northern hemisphere because of differences in the relative production of fresh-

water and marine habitats (Gross et al. 1988). Northern marine environments, where fish with anadromous life histories prevail, are more productive than freshwater environments. In more southern environments where production of freshwater systems is greater, fish with catadromous life histories prevail (i.e., begin life in the marine environment, move to freshwater to grow and mature and return the marine environment to reproduce). Fish with catadromous life histories are not found in the Pacific coastal ecoregion.

Large annual fluctuations in stream habitat conditions also contribute to the predominance of anadromous species in the Pacific coastal ecoregion. Flows vary by several orders of magnitude annually (10–1,000 m<sup>3</sup>/sec) and many streams experience wide fluctuations in water temperature. Fish must survive until they are able to reproduce, and then they must reproduce successfully to be successful in such an environment. Successful reproduction is more

likely in fish that are highly fecund and have relatively large bodies capable of burying eggs deeper in substrate.

### Population Variability

What the Pacific coastal ecoregion lacks in species diversity, is at least partially compensated in variability within and among local watershed populations. Fish populations vary phenotypically and genetically to a substantial degree. Species or populations can exhibit multiple life history patterns. For example, chinook salmon (*O. tshawytscha*) exhibit two types of general life histories. The stream type rear in fresh water for a year or more as juveniles and may enter fresh water many months prior to spawning as adults, whereas the ocean type rear in streams for only a few months as juveniles before migrating to sea and spawn shortly after reentering freshwater as adults. When both types of chinook are present in rivers, the two are often temporally and spatially isolated in terms of reproduction. Stream-type chinook often use headwater areas for spawning and rearing, and spawn in the early fall. Ocean types spawn in the late fall and rear lower in the drainage system (Healey 1991). Chinook salmon may exhibit multiple life histories even within a single population. Reimers (1973)

identified five distinct life history variations within a population of ocean-type chinook salmon in Oregon's Sixes River. These variations centered around the length of time spent in headwater tributaries, the river mainstem, and the estuary, and were adaptations to highly unpredictable rearing conditions in the Sixes River system and in the ocean. Thus, for species with extended freshwater spawning and rearing periods (such as chinook and coho salmon, steelhead, and sea-run cutthroat trout) different life history patterns are favored as environmental conditions change from year to year (Healey 1991, Healey and Prince 1995, Stouder et al. 1996). It is likely that life history polymorphism within populations has both genetic and environmental components.

Genetic and phenotypic variation, within and between stream fish populations, indicates that although each population may contain most of the genetic material for the species, phenotype expressed as adaptation to local conditions is remarkably plastic (Table 9.4) (Healey and Prince 1995). The genetic and environmental basis of this variability is complex, but the great majority of evidence points to strong selective tendencies for local adaptation.

Spawning populations of anadromous salmon exhibit highly specific local adaptations for a number of traits such as the complicated

TABLE 9.4. Percentage of genotypic and phenotypic variation of anadromous salmonids within populations, among populations within regions, and among regions.

Species and characteristic	Variation (%)		
	Within populations	Among populations	Among regions
Chinook			
Allozyme variation <sup>a</sup>	87.7	4.6	7.7
Allozyme variation <sup>b</sup>	94.1	3.3	2.6
Pink <sup>c</sup>			
Fry length	30.3	41.4	28.2
Adult weight	13.3	1.5	85.2
Chum <sup>c</sup>			
Fecundity	7.9	5.1	87.0
Age at maturity	14.0	0.5	85.5

<sup>a</sup> Utter et al. (1989).

<sup>b</sup> Gharrett et al. (1987).

<sup>c</sup> Groot and Margolis (1991).

From Healey and Prince 1995.

homing behavior, temperature adjustments, unique local mating behavior, and adjustments of smolts to local feeding conditions. These adaptations are most likely to be quantitative characteristics that are dependent on the effects of many genes, each of which has only a small effect individually (polygenes)—it would likely be difficult to “replace” a local population with transplants from nonlocal populations. Therefore, the more complex the life cycle, the more difficult it would be to replace a local population (NRC 1996).

In fact, attempts to establish Pacific salmon elsewhere often have been unsuccessful. Yet, in a few instances, populations have been successfully transplanted and adaptive radiation has occurred quickly. A dramatic example of the ability of anadromous salmonids to adapt to local conditions is demonstrated by the phenotypic divergence of chinook salmon in several rivers on the South Island of New Zealand, where several distinct life history patterns developed after introduction of this species from a single Sacramento River donor population about 90 years ago (Quinn and Unwin 1993). The degree of phenotypic differentiation that developed over a span of about 20 generations may be among the highest known for aquatic vertebrates (Miller 1961) and indicates that under certain conditions significant evolutionary divergence can occur in a matter of decades (Healey and Prince 1995).

The extent to which populations of fishes other than anadromous salmonids have developed unique genetic, morphological, and life history characteristics in Pacific Northwest rivers is not nearly as well known. Non-anadromous species may not have differentiated into “stocks” to the degree exhibited by Pacific salmon but available evidence suggests that significant variation among populations is the rule rather than the exception, particularly for those species with widespread distributions. Examples of non-anadromous taxa possessing locally variable populations include lampreys (*Lampetra* spp.; Kan 1975), speckled dace (*Rhinichthys osculus*; Zirges 1973, Sada et al. 1995), longnose dace (*R. cataractae*; Bisson and Reimers 1977), suckers (*Catostomus* and other genera; Smith 1966), sculpins (*Cottus* spp;

McAllister and Lindsey 1961, Bond 1963), and threespine sticklebacks (*Gasterosteus aculeatus*; Miller and Hubbs 1969, Hagen and Gilbertson 1972).

Virtually every study comparing variability among populations of Pacific coastal freshwater fishes over relatively large areas reports significant variation in some morphological feature. For example, there are strong differences in body size, morphology and egg size of chum salmon (*O. keta*) in British Columbia rivers (Beacham and Murray 1987). Individuals of populations from larger rivers have larger heads, thicker caudal peduncles, and larger fins than those from smaller rivers, and early spawning populations have older fish, larger eggs, and later emerging fry than later spawning groups. These characteristics appear to be adaptations to local conditions. Fish in larger rivers need to move larger substrates and deposit eggs deeper than fish spawning in smaller streams.

Local populations of the same species may also exhibit variation in morphologies and life histories. For example, anadromous forms of the threespine stickleback are generally larger and have higher gill raker, fin ray, and lateral plate counts than resident (i.e., nonanadromous) forms (Bell 1984). In coastal areas of northern California, morphological differences of threespine stickleback are not as well defined (Snyder and Dingle 1989), but there are differences in life history features of the two types. Anadromous forms are older and larger when they first reproduce and more fecund than resident forms. Juvenile coho salmon (*O. kisutch*) from a lake and inlet stream in British Columbia exhibit differences in behavior and morphology (Swain and Holtby 1989). The stream fish are more aggressive than lake-rearing individuals; as juveniles stream fish are territorial. Lake fish have more posteriorly placed pectoral fins, shallower bodies, and smaller, less colorful dorsal and anal fins than stream fish. Their diminished aggression and accompanying body features are an adaptation to schooling behavior in open waters.

Reasons for such variability are complex. Some variation may be the result of founder

effects (establishment of a new population by a few original founders which carry only a small fraction of the total genetic variation of the parental population); some may be caused by local selective pressures coupled with prolonged geographical isolation. But whatever the reasons, morphological, physiological, and life history characteristics of fishes in this region can change fairly rapidly. Protecting this local variability in morphological, physiological, and life history characteristics among and within local populations is at the heart of applying the "evolutionarily significant unit" (populations of anadromous salmonids that share common genetic and/or life history features and are a unit of consideration for the Endangered Species Act listing) approach to the definition of distinct population segments under the Endangered Species Act (Waples 1991) and is strongly endorsed by the National Research Council (NRC 1996).

## Watershed Scale Patterns of Diversity

Generally, the diversity of stream fish communities increases from headwaters to lower portions of river basins. That is, within a drainage basin the number of species increases in higher-order channels (i.e., larger streams). This pattern has been observed in the United States in the midwest (Horwitz 1978, Schlosser 1987), in the south (Boschung 1987), and in the east (Sheldon 1968). However, it has not been well established in the Pacific coastal ecoregion, primarily because most studies of stream fishes in the region have focused on salmonids rather than other species, nor have the longitudinal distribution of stream fishes been considered. Nonetheless, Li et al. (1987) described a generalized distribution of fish (salmonids and other species) in river systems of the Pacific coastal ecoregion (Figure 9.2) which follows the diversity pattern described above. In addition, when the number of species (and collection locations) is plotted relative to elevation (a surrogate for stream size and basin area) for four different river systems in Oregon and there is a

significant ( $p < 0.05$ ) negative correlation between numbers of species collected and elevation (Figure 9.3). These examples suggest that the pattern of increasing species richness with stream order holds in the Pacific coastal ecoregion.

## Ecological Rules

Strictly from a species richness perspective, the general pattern of increasing species diversity moving down a watershed fits the *species-area relationship* of community ecology. Simply stated, this concept, which has been established for more than a century, predicts that the number of species increases with the area considered (Williams 1964). Rosenzweig (1994) cited studies on a suite of organisms where this relationship holds and characterized it as the "most supported rule in ecology." However, the species-area relationship may break down at large-spatial scales, such as regions, when there are large differences in productivity across an area (Levin 1974). Caution should be used in interpreting species-area relationships at smaller spatial scales, such as watersheds, because species numbers can be influenced by factors such as rates of disturbance and competition, and regional processes such as speciation and biogeographical dispersal (Ricklefs 1987, Caswell and Cohen 1993).

Another possible explanation for the observed patterns in fish distribution at the watershed scale is that diversity is related to productivity (Connell and Orias 1964, McArthur and Pianka 1966, Currie 1991, Huston 1994). Diversity is generally greatest at intermediate levels of productivity. It declines at lower and higher levels of productivity (Rosenzweig and Abramsky 1993, see also Chapter 17). The reason for this pattern is the subject of much debate in ecology. Rosenzweig and Abramsky (1993) believe that the most plausible explanation is that resource and habitat heterogeneity is greatest at intermediate levels of productivity. Increased heterogeneity allows for greater diversity. The productivity rule is most applicable at large spatial scales ( $10^6 \text{ km}^2$ ) (Wright et al. 1993). It also depends on taxonomic scale; the relationship is

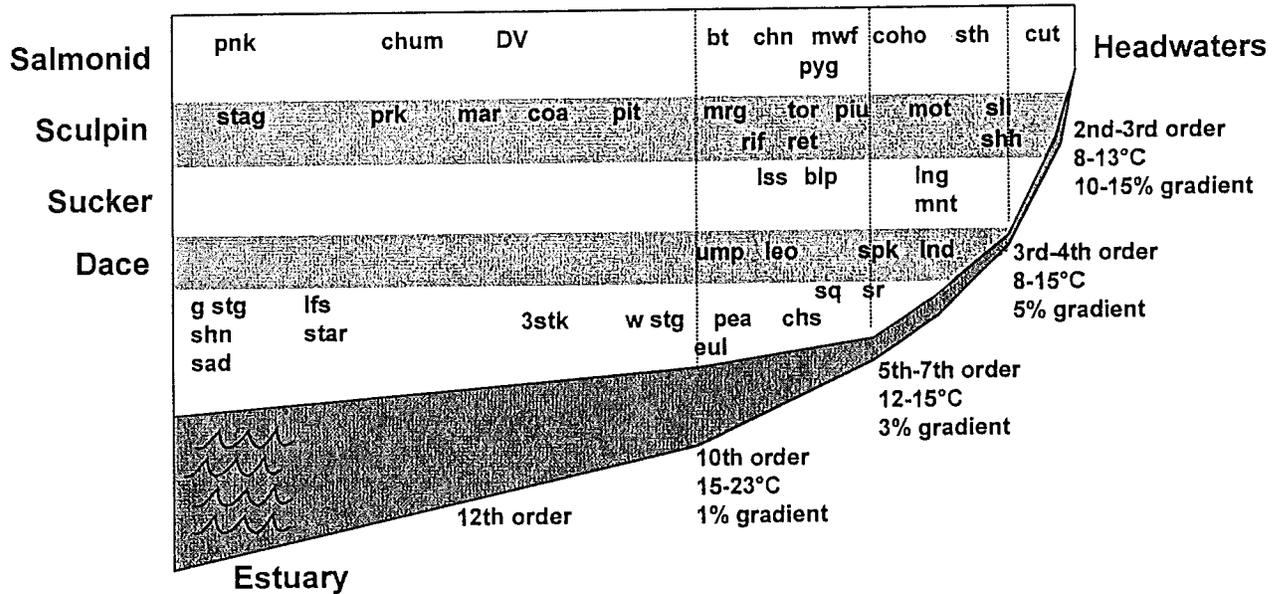


FIGURE 9.2. Generalized distribution of native fishes throughout watersheds along a continuum of gradient, stream order, and water temperature (from Li et al. 1987 © University of Oklahoma Press, with permission).

bt = bull trout  
 chn = chinook salmon  
 cut = cutthroat trout  
 eul = eulechon  
 lfs = longfin smelt  
 lss = largescale sculpin  
 mot = mottled sculpin  
 pea = peamouth  
 pink = pink salmon  
 ret = reticulate sculpin  
 shh = shorthead sculpin  
 spk = speckled dace  
 stag = staghorn sculpin  
 3 stk = threespined stickleback  
 w stg = white sturgeon

blp = bridgelip sucker  
 chs = chiselmouth  
 coho = coho salmon  
 g stg = green sturgeon  
 lng = longnose sucker  
 mar = marbled sculpin  
 mrg = margined sculpin  
 pit = pit sculpin  
 prk = prickly sculpin  
 rif = riffle sculpin  
 shin = shiner perch  
 sq = squawfish  
 star = starry flounder  
 tor = torrent sculpin

chum = chum salmon  
 coa = coast range sculpin  
 DV = Dolly Varden  
 leo = leopard dace  
 lng = longnose dace  
 mnt = mountain sucker  
 mwf = mountain whitefish  
 piu = piute sculpin  
 pyg = pygmy whitefish  
 sad = saddleback gunnel  
 sli = slimy sculpin  
 sr = sandroller  
 sth = steelhead trout  
 ump = Umpqua dace

weaker at lower taxonomic levels (i.e., family and genus) (Wright et al. 1993). Rosenzweig and Abramsky (1993) and Rosenzweig (1994) reviewed the applicability of this rule and concluded that it generally held in terrestrial systems but was less applicable in aquatic systems. The reason for this is not known.

Further, the River Continuum Concept (Vannote et al. 1980, Chapter 1), which predicts changes in biological and physical attributes in stream systems moving from headwaters to larger rivers (Table 9.5), implies that the productivity rule is less applicable because other aspects of aquatic systems also influence diversity. In other words, the pattern of downstream

change in biotic communities (e.g., downstream increase of fish species) is influenced, not only by changes in energy input and processing but also by changes in physical features such as width, depth, flow velocity and volume, and temperature.

### Physical and Biological Processes

Within a watershed, biological (biotic: e.g., competition and predation) and physical (abiotic: e.g., flow, pool depth, etc.) processes strongly influence the structure and composition of fish communities. The relative influence of physical and biological processes varies

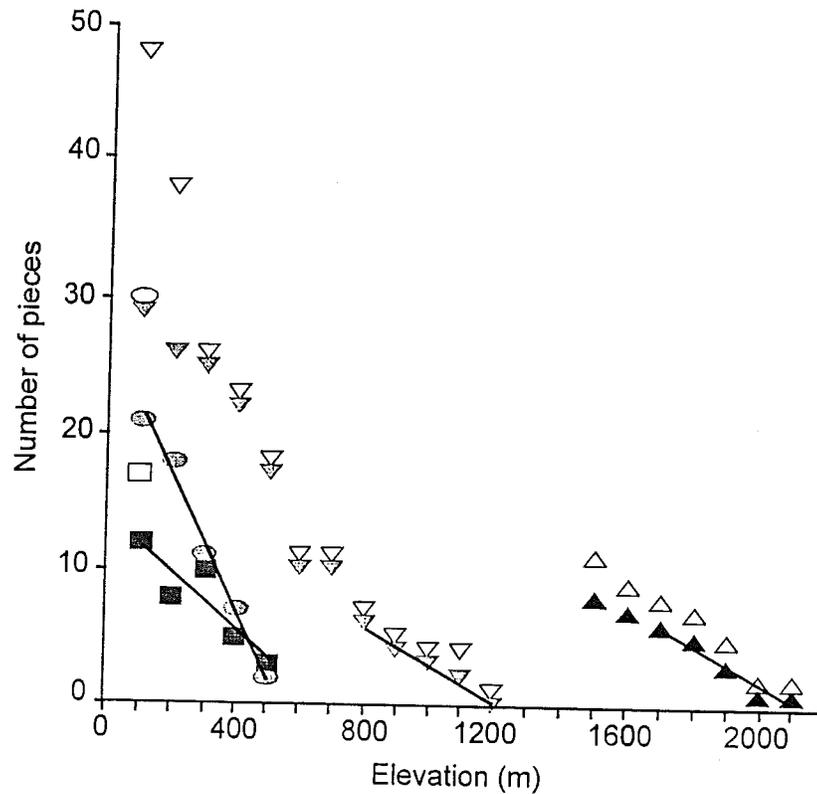


FIGURE 9.3. Relationship between basin elevation and number of fish species for four Oregon watersheds. (North Coast = ■; South Coast = ●;

Willamette = ▼; Goose Lake = ▲). Solid symbols are native fishes and open symbols are introduced species.

along the stream network (Figure 9.4). Schlosser (1987) proposed a conceptual framework to explain how fish communities in warmwater streams are structured based on the relationship between changes in habitat heterogeneity (i.e., the diversity of habitat types and the complexity of habitat conditions), and the

strength and type of biotic processes in different parts of the watershed (Figure 9.5). For example, according to Schlosser's framework, habitat heterogeneity is low in headwaters (although annual physical conditions, such as flow and pool depth, are more variable), primarily because deep pools are lacking and competi-

TABLE 9.5. Summary of basin features predicted by the River Continuum Concept.

Feature	Location		
	Headwaters (1st-3rd order)	Medium-sized streams (4th-6th order)	Large rivers (>6th order)
Energy Source	Allochthonous detritus	Autochthonous primary production	Autochthonous primary production
Production-respiration ratio	<1	>1	>1
Riparian vegetation influence	Strong	Moderate	Weak, localized
Benthic macroinvertebrate Functional feeding group	Shredders	Collectors	Collectors
Fish	Collectors Insectivores	Grazers Piscivores, Insectivores	Piscivores, Insectivores, Planktivores

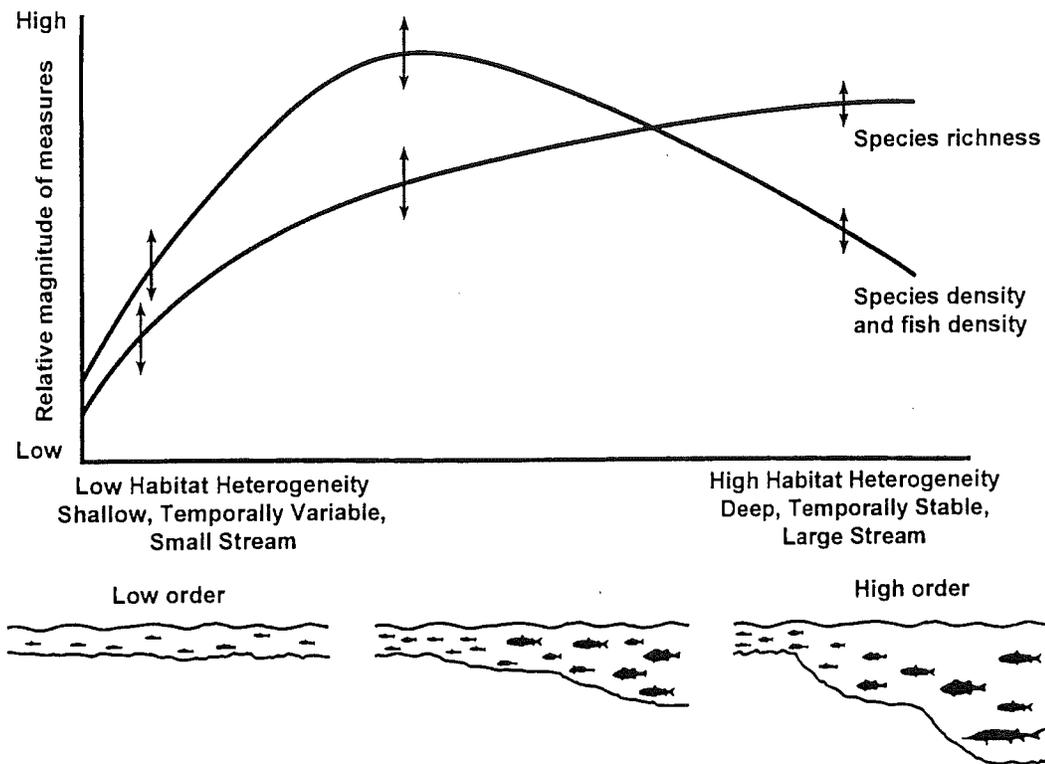


FIGURE 9.4. Hypothetical pattern of fish community attributes along a gradient of increasing habitat heterogeneity and pool development in a small warmwater stream. The patterns of species composition and size structure of fishes in the community are

shown at the bottom of the figure. Arrows indicate the relative temporal variability in the parameters (from Schlosser 1987 © University of Oklahoma Press with permission).

tion is the dominant biotic process. Consequently, the number of species is low and trophic relationships are simple compared to other parts of the system. Fish communities in these streams demonstrate high variability in numbers and relative abundance as a result of the large variability in conditions and lack of refugia (Schlosser 1987). Headwater fishes are able to persist, in part, because of the ability to recolonize areas quickly following a disturbance. These fishes have high fecundity rates and mobile juveniles. Schlosser's (1987) framework further predicts that habitat heterogeneity and community diversity continues to increase as stream size and order increase (Figure 9.4). In larger rivers, the relative influence of biotic processes may be greater than in other parts of the watershed (Schlosser 1987). For example, piscivores (i.e., fish that feed predominately on other fish) are a dominant component of the community and presumably are responsible, in part, for the decline of smaller headwater species. The structure and composition of fish communities are more stable than

communities in headwater streams because of decreased variability in environmental conditions in larger streams.

It is not clear how applicable Schlosser's (1987) framework is to fish communities in Pacific coastal ecoregion streams, particularly with regard to the relative importance of biotic and abiotic factors. Although studies of the relative importance of biological and physical processes to fish community structure in Pacific coastal streams are lacking, the pattern of distribution presented by Li et al. (1987) appears to follow the pattern (Figure 9.2) (for at least a large portion of the basin) described by Schlosser (1987) (Figure 9.5) and Vannote et al. (1980) (Table 9.5). However, in large rivers (i.e. >10th order), numbers of native fish species appear to decline, possibly because fewer niches are available in these more homogenous habitats.

Fish communities in Pacific coastal ecoregion headwater streams tend to be relatively less diverse compared to lower parts of the stream network. Typical communities have a high

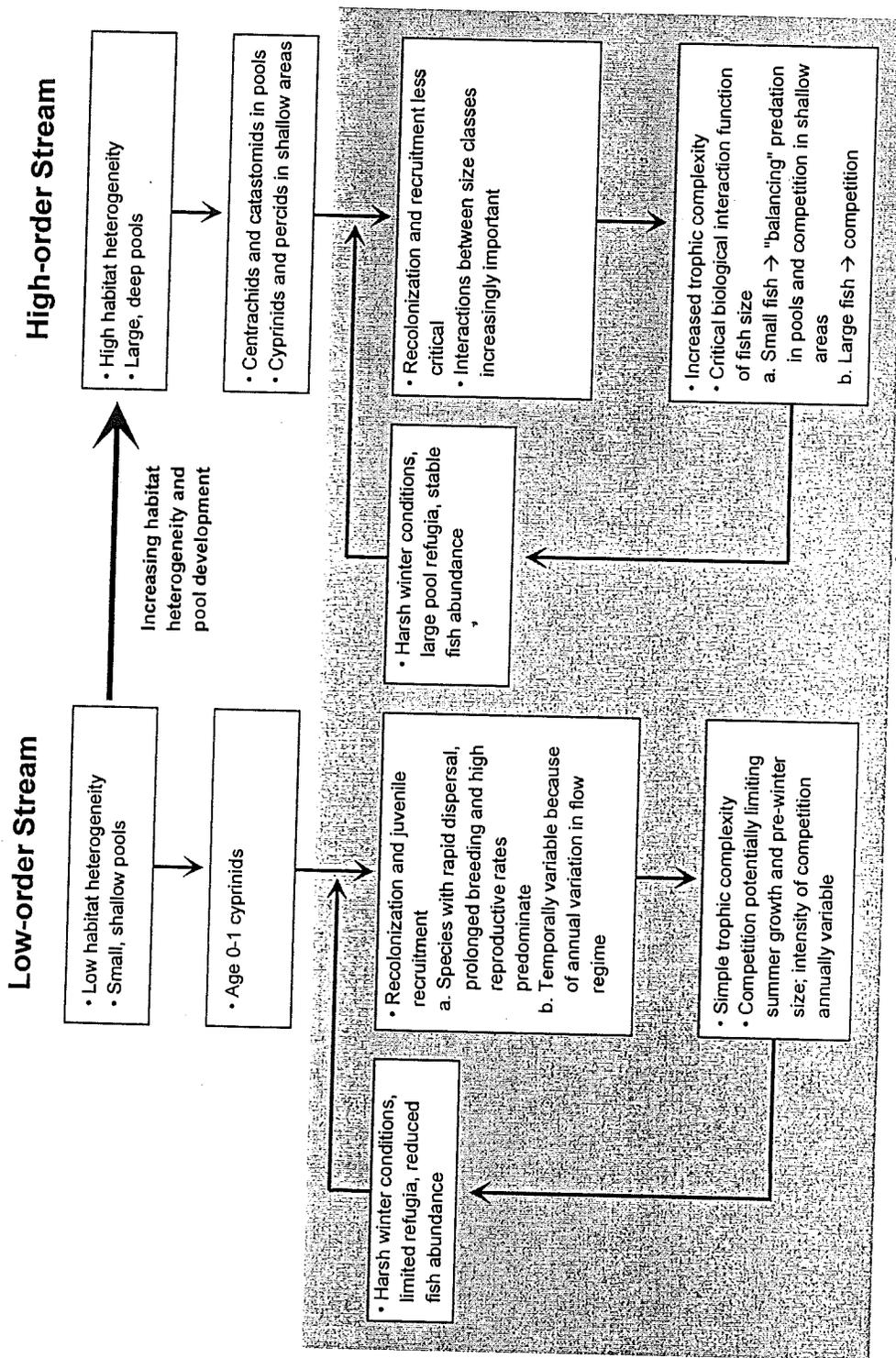


FIGURE 9.5. Conceptual framework of processes determining fish community structure along a gradient of habitat heterogeneity and pool development in a small warmwater stream. Critical ecological processes are outlined in shaded boxes (from Schlosser 1987 © University of Oklahoma Press, with permission).

degree of trophic and microhabitat segregation (Moyle and Herbold 1987) and contain one or two species of lamprey, trout, dace, and sculpin—fishes with very different morphologies and behaviors (Moyle and Cech 1982). Salmonids have very agile, torpedo-shaped bodies that allow them to occupy foraging

positions in the water column and swim in rapid bursts (Moyle and Cech 1982) (Figure 9.6a). They actively prey on benthic macroinvertebrates, terrestrial insects, and fishes. Dace are active bottom dwellers with small subterminal mouths and feed on benthic organisms (Figure 9.6b). Sculpins are bottom

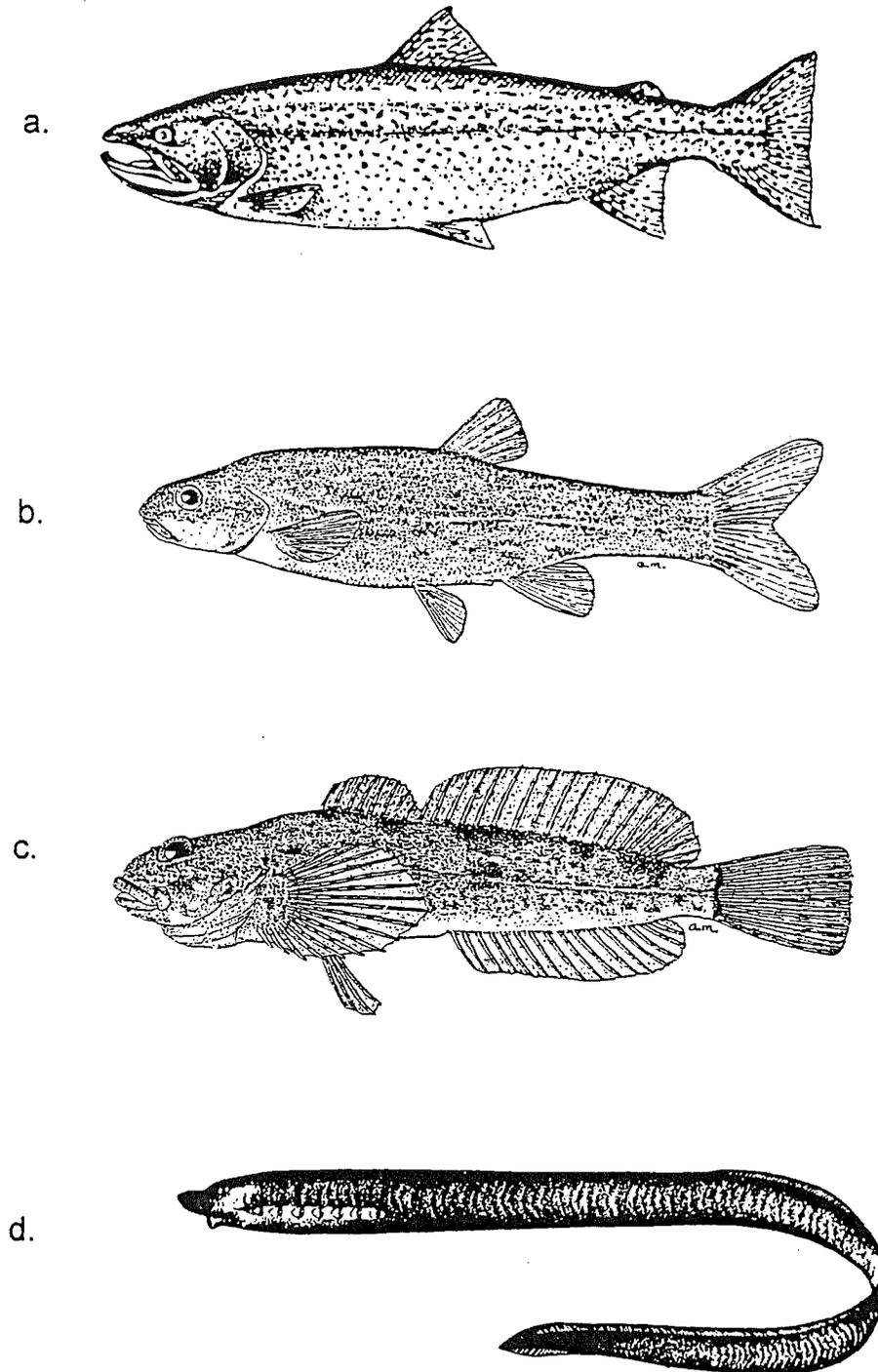


FIGURE 9.6. Fishes (a = cutthroat trout, b = speckled dace, c = riffle sculpin, and d = western brook lamprey) found in headwater streams in the Pacific coastal ecoregion.

dwellers with dorsoventrally flattened bodies and large pectoral fins and mouths; they ambush their prey (benthic macroinvertebrates and fish) (Figure 9.6c). Lamprey ammocoetes (i.e., immature forms) have vermiform bodies that can burrow in stream substrates (Figure 9.6d). As a result of these differences in morphology and behavior, biological factors, (particularly competition) have little influence on the community structure and composition (Zalewski and Naiman 1985). Thus, physical factors related to the dynamic nature of these streams, low habitat heterogeneity, and restricted temperature regimes are the most important influences on fish community structure, particularly in headwater streams.

Schlosser (1987) predicts that more diverse communities develop moving downstream (Figure 9.5). Environmental conditions tend to be less variable than in headwaters. Habitat heterogeneity and numbers of larger, deeper pools increases in downstream, high-order channels. Many headwater species also may be present downstream. However, the age classes of the species present differ between the two areas; headwaters primarily contain juveniles and downstream areas primarily contain adults (Figure 9.5). Predation, particularly on smaller individuals, and competition are the dominant processes influencing community structure in downstream areas.

Differences in temporal and localized distribution of fish allow similar species to coexist in the different parts of the drainage network. Where the distribution of congeneric species such as anadromous salmonids overlap, differences in fine-scale distributions and timing of activities limit interactions for particular resources. For example, in smaller watersheds (i.e., 4th–5th order streams, as in Fish Creek, Oregon) coho salmon, winter and summer steelhead trout, and spring chinook salmon use the same parts of the basin for spawning and early rearing (Figure 9.7). However, chinook and coho salmon use larger size gravels for spawning (1.3–10.0 cm diameter) than steelhead trout (0.6–10.0 cm) (Bjornn and Reiser 1991). Chinook salmon and steelhead trout generally use deeper areas ( $\geq 24$  cm) for spawning than coho salmon ( $\geq 18$  cm). Further, these

species spawn at different times which results in the temporal segregation of juveniles when habitat requirements overlap. Chinook salmon spawn from mid-September to mid-November, coho salmon from mid-October to mid-January, summer steelhead trout from December to May, and winter steelhead trout from mid-March to late-June (Figure 9.8). The temporal and fine-scale partitioning of habitats allows similar species to use particular habitats and thus increases species richness and diversity.

Differences in the rates of species additions observed in Figure 9.3 can be attributed to various factors; for example, variations in basin morphology and water temperature. Stream gradient and size most strongly mediate the rate of species additions in the North and South Coast streams, whereas water temperature is a stronger influence in higher elevation headwater streams. Numbers of fish species increase at a significantly higher rate (2.1 and 4.9 species/100 m drop in elevation, respectively;  $p < 0.01$ ) in the low elevation headwaters in the North and South Coast streams in Oregon, than in the higher elevation headwaters in the Willamette River (1.4 species/100 m drop in elevation) and Goose Lake watershed (1.4 species/100 m drop in elevation) (Figure 9.3). The influence of cold water is more extensive in the higher elevation streams and may limit additions of species preferring warmer water. Another factor that affects the rate of species additions is the influence of different zoogeographic provinces, or life zones. For example, the high rates of species additions in the South Coast streams is likely due to the fact that the area encompasses three different zoogeographic provinces.

## Reach Scale Diversity

The structure and composition of aquatic biotic communities also varies with reach-level characteristics. A reach is an integrated series of geomorphic units sharing a common landform pattern (Grant et al. 1990). Reaches are influenced by variation in channel slope, local side slopes, valley floor width, riparian vegetation,

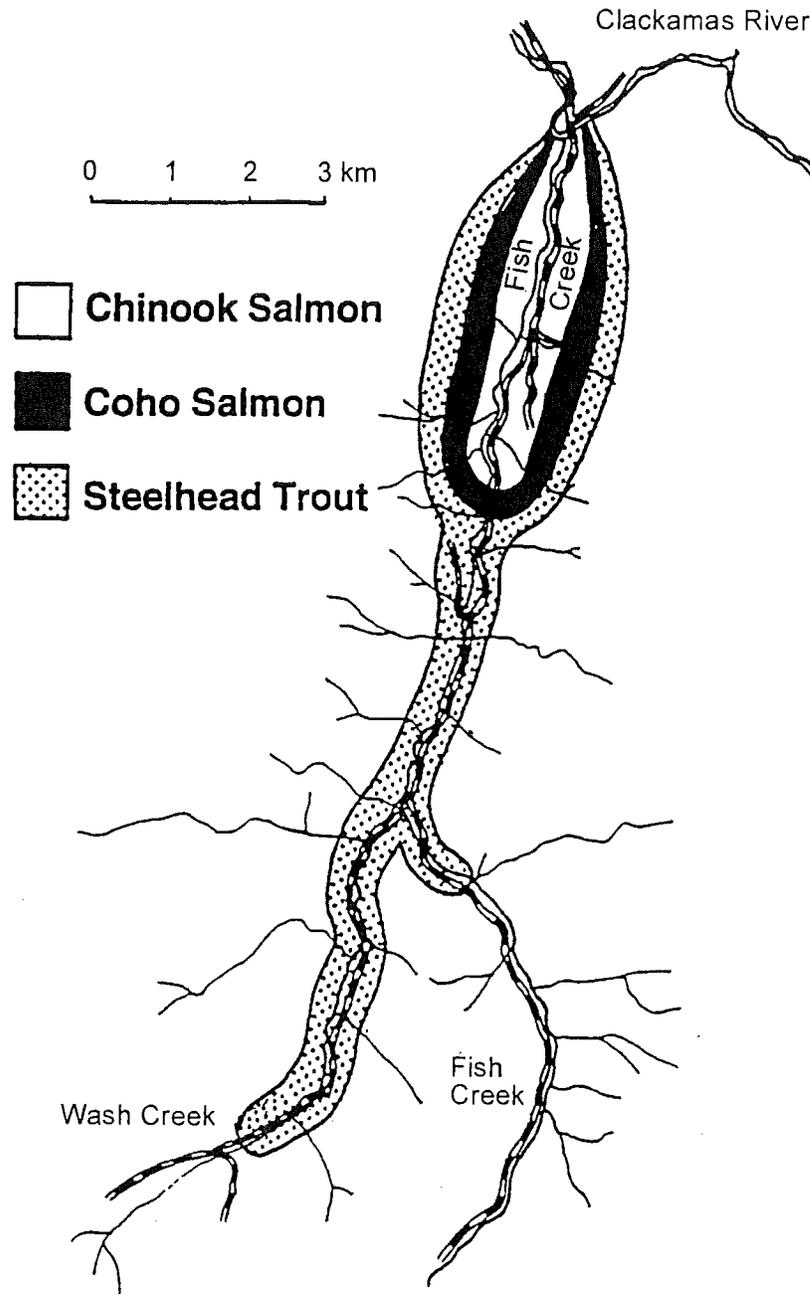


FIGURE 9.7. Spawning and early rearing distribution of anadromous salmonids in Fish Creek, Oregon.

and bank material (Frissell et al. 1986). Gregory et al. (1989) classified reaches as constrained (active channel to valley floor width ratio  $<2$ ) and unconstrained (active channel to valley floor width ratio  $>2$ ) (Figure 9.9a and 9.9b).

In several small coastal Oregon streams, salmonid community composition varies between these two reach types (Reeves, unpublished data). Trout (age 1+) are generally the

dominant component of the community in constrained reaches (Figure 9.10a). In unconstrained reaches salmon (coho and chinook) and trout (age 1+) are more evenly distributed in terms of relative abundance (Figure 9.10b). In the Elk River, Oregon, unconstrained reaches contain approximately 15% of the total available habitat but accounted for 30% of the estimated juvenile anadromous salmonids. In southwestern Washington streams, Cupp

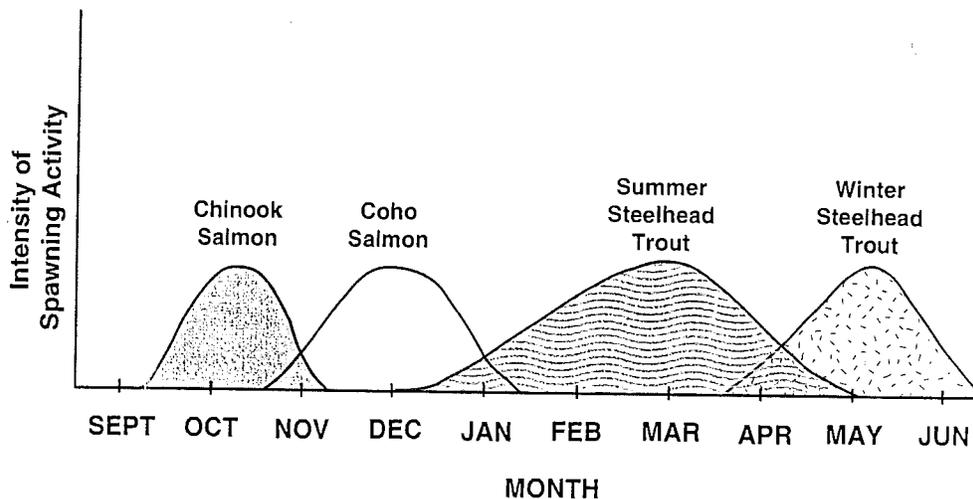


FIGURE 9.8. Spawning intensity and duration of anadromous salmonids in Fish Creek, Oregon.

(1989) found the greatest abundance of salmonids in lower elevation, lower gradient stream reaches with wide valleys. In unconstrained reaches of the McKenzie River headwaters in Oregon densities of cutthroat and rainbow trout are more than twice those in constrained reaches (Gregory et al. 1989).

This pattern, however, may not apply to lower portions of large watersheds. The relationship between reach features and salmonid communities varies with location in the stream network in Drift Creek, Oregon (drainage area 140 km<sup>2</sup>) (Schwartz 1990). In the mainstem of Drift Creek there is no clear pattern of commu-

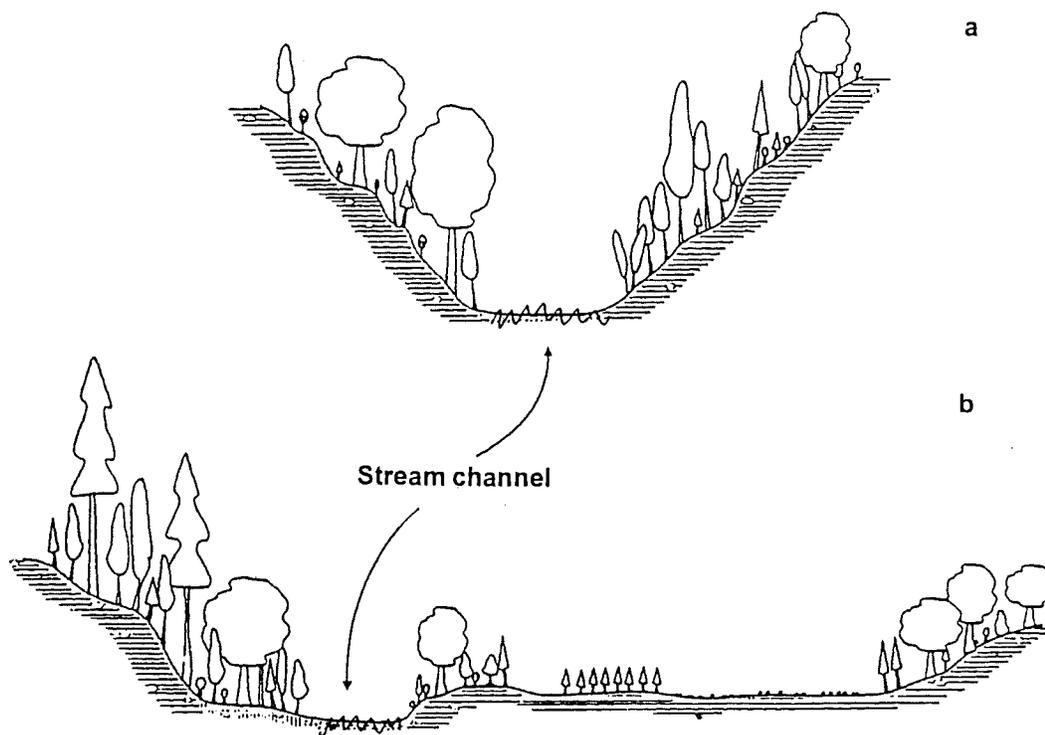
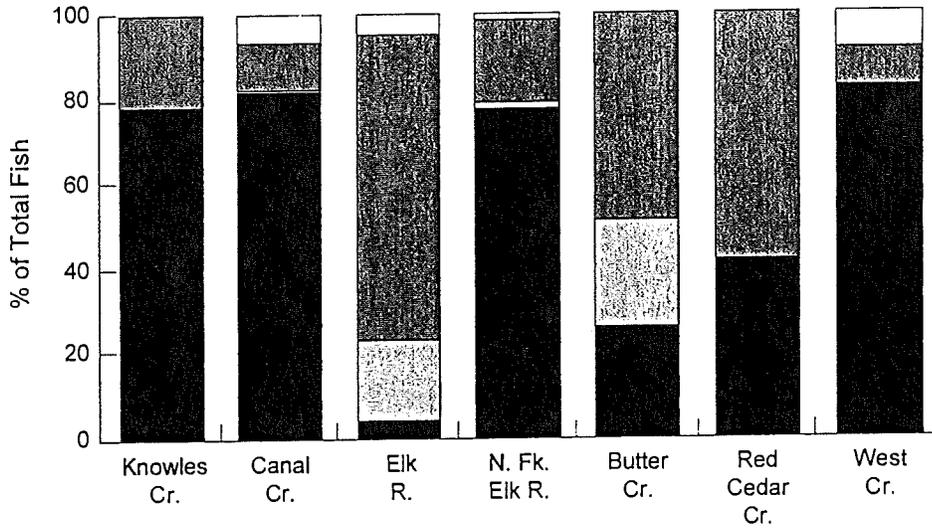


FIGURE 9.9. Generalized diagram of (a) constrained and (b) unconstrained reaches of streams in the Pacific coastal ecoregion.

a. Unconstrained



b. Constrained

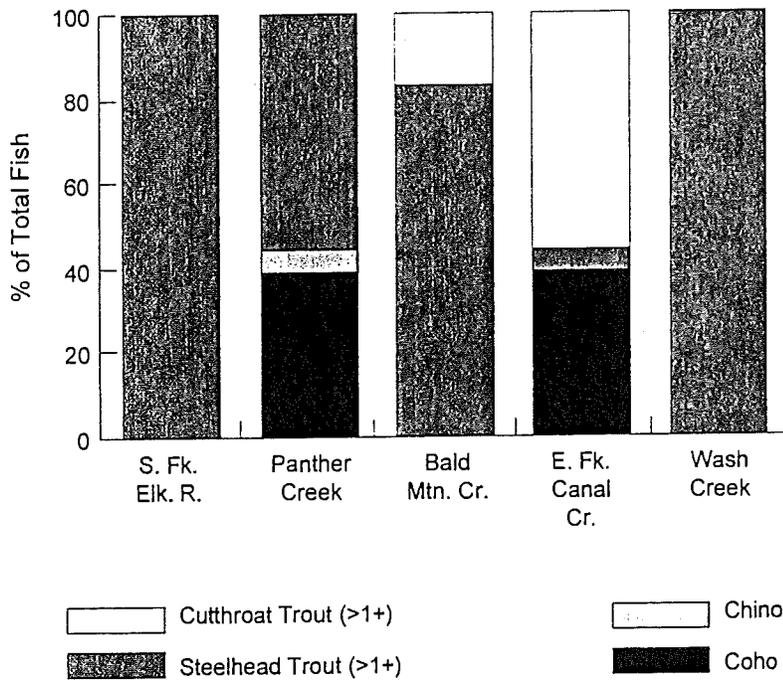


FIGURE 9.10. Composition of juvenile anadromous salmonid assemblages in (a) constrained and (b) unconstrained Oregon coastal streams.

nity structure with regard to reach types. Communities of juvenile anadromous salmonids in unconstrained and constrained reaches contained salmon and trout in about the same relative abundance. In tributaries, however, higher gradient constrained reaches are dominated by

trout; whereas, lower gradient, unconstrained reaches contain salmon and trout.

Several factors explain the differences in the salmonid communities in the different reach types. Unconstrained reaches contain a greater diversity of habitat types than constrained

reaches (Gregory et al. 1989, Schwartz 1990). Constrained reaches are typically dominated by fast water habitat and offer little refugia from high flow events, whereas, unconstrained reaches contain slow water (e.g., pools and side channels) and fast water (e.g., riffles) habitat and provide lateral refuges during floods.

Fish community diversity and production are positively correlated at the reach scale. Primary and secondary production are generally greater in unconstrained reaches than in constrained reaches. For example, primary production and densities of benthic macroinvertebrates are higher in unconstrained reaches of Elk River than in constrained reaches (Zucker 1993). Unconstrained reaches are also sites of greater hyporheic zone exchange (Grimm and Fisher 1984, Triska et al. 1989, Chapter 16) and greater hydraulic and particulate organic matter retention (Lamberti et al. 1989), factors which contribute to higher production and, therefore, a greater potential for diversity.

## Habitat Unit Patterns of Diversity

Diversity of fish species is directly related to habitat unit features. There are two primary types of habitat units: riffles, which are topographic high points in the bed profile and are composed of coarser sediments, and pools which are low points with finer substrates (Richards 1982, O'Neill and Abrahams 1987). At base flows, riffles are shallow and have a steep water-surface gradient with rapid flow. In contrast, pools are deeper and generally have a gentle surface slope with slower flow (O'Neill and Abrahams 1987, Richards 1978).

Riffles and pools do not always have clear boundaries, but they are distinct ecological habitats. Fish inhabiting them differ markedly in taxonomic composition and morphological, physiological, and behavioral traits. Riffle dwellers (e.g., sculpins, dace, and age 0+ trout) are bottom-oriented fish, possessing large pectoral fins to help maintain position. Some lack an air bladder or can adjust the air in the swim bladder to reduce buoyancy. Riffle dwellers are

solitary or part of small loose knit groups. Pool dwellers (e.g., coho salmon), often found in aggregations, are more active swimmers with more dorsally-ventrally compressed bodies and smaller fins.

Within a habitat unit, structural features, substrate, flow velocity, and pool depth influence biotic diversity (Sheldon 1968, Evans and Noble 1979, Angermeier 1987). Increased complexity resulting from the combination of these factors creates a greater array of microhabitats. Complexity can mediate competition between species. Structural complexity provides protection from predators, alters foraging efficiency (Wilzbach 1985), and influences social interactions (Fausch and White 1981, Glova 1986). In a Washington stream, Lonzarich and Quinn (1995) observed a general increase in species diversity with increasing complexity of pools and different responses of species to habitat features. Numbers of juvenile coho salmon, steelhead trout (age 1+), and cutthroat trout were directly correlated with depth; however, sculpin (*C. aleuticus*) did not respond to changes in habitat features. A similar pattern for salmonids and habitat features has been observed in a small coastal Oregon stream (D.H. Olson, personal communication, USDA Forest Service, Pacific Northwest Research Station, Corvallis, Oregon). In that stream, salmonid diversity (Shannon-Weiner Index, see Chapter 17) increased with maximum pool depth, pool surface area, and volume of wood. Community diversity increases during the summer with increasing levels of habitat complexity (S. Feith and S.V. Gregory, personal communication, Department of Fisheries and Wildlife, Oregon State University, Corvallis, Oregon). In another small stream in western Oregon, biomass (an indicator of abundance) of speckled dace, sculpins (*C. perplexus* and *C. gulosus*), and juvenile cutthroat trout also increased with increasing levels of habitat complexity. However, biomass of coho salmon showed no response to the changes in habitat complexity even though habitat complexity may influence coho density at other seasons (Nickelson et al. 1992, Quinn and Peterson 1996) and life history stages (McMahon and Holtby 1992).

Complexity within habitat units also influences the diversity of fish assemblages (Gorman and Karr 1978, Schlosser 1982, Angermeier and Karr 1984). Reduced habitat complexity, resulting primarily from the loss of large wood, in part, explains differences in juvenile anadromous salmonid communities in coastal Oregon streams with varying levels of timber harvest activity (Reeves et al. 1993). Communities in streams with reduced habitat complexity are less diverse than those with higher habitat complexity. In addition, interactions between coho salmon and steelhead and cutthroat trout may be altered as a result of habitat simplification. Further, changes in microhabitat features favors some species but decreases suitability for others. For example, densities of fish decrease in southeastern Alaska and mid-western streams when habitat structure is removed or simplified (Dolloff 1986, Elliott 1986, Berkman and Rabeni 1987).

Location of a habitat unit in the stream network also influences community diversity within the unit. As discussed previously, diversity of stream fish communities tends to increase downstream (Figures 9.2 and 9.3). A major reason for this is that pool depth also increases creating, among other things, a greater array of microhabitats which results in the addition of species (Sheldon 1968, Schlosser 1987). However, at present the role of habitat unit size, complexity, and location is only understood for small streams.

The influence of biological factors, such as competition and predation, on the structure and composition of fish communities in habitat units of streams is largely unknown at present. Studies that have examined interactions between species have focused on salmonids. Surprisingly, virtually nothing is known about interactions between salmonids and nonsalmonids, or among nonsalmonids, in the Pacific coastal ecoregion. Researchers in other regions have found that the influence of competition on community diversity varies depending on local conditions (Fausch and White 1981, Matthews 1982, Schlosser and Toth 1984, Moyle and Vondracek 1985, Grossman and Freeman 1987, Dolloff and Reeves 1990, Grossman and Boule 1991).

Two forms of interactions have been identified for stream fishes, interactive and selective segregation (Nilsson 1967). In *interactive segregation*, species are capable of using the same niche but one species is dominant and precludes the subordinate species from preferred habitats. The dominant species is generally more aggressive or more efficient at exploiting a particular resource. Thus, the subordinate species will move into the preferred habitat only when the dominant species is absent. Habitat use by juvenile coho salmon and trout (age 1+) is influenced, in part, by interactions among these species. Coho salmon are aggressive and preclude steelhead (Hartman 1965) and cutthroat trout (Glova 1978) from the head of pools, where food resources are highest. Steelhead trout dominate cutthroat trout and generally preclude them from habitats in larger stream systems (i.e., >15 km<sup>2</sup>) in British Columbia (Hartman and Gill 1968). Similar patterns of segregation have been observed between rainbow and cutthroat trout (Nilsson and Northcote 1981) and cutthroat and Dolly Varden (Andrusak and Northcote 1971, Hindar et al. 1988) in lakes. Reeves et al. (1987) found that habitat use by redbreast shiner and juvenile steelhead trout was determined by interactive segregation. Under cool water temperatures (i.e., <20°C), steelhead trout precluded shiners from riffles, where food is most abundant, by aggressively driving the shiners away. Shiners formed loose aggregations in pools in the presence of trout. When trout were absent, shiners moved to riffles.

In contrast to interactive segregation, *selective segregation* involves differential use of available resources by each species (Nilsson 1967). Each species uses resources not "selected" by the other, resulting in neutral interactions among groups. Differences in resource use can arise from differences in instinctive behavior or body morphology. For example, selective segregation between juvenile steelhead trout and chinook salmon reduces interactions for habitat and food in Idaho streams (Everest and Chapman 1972). The fish use similar habitats at any given size but, because of differences in life history features, interactions for space are minimal. In this case, because

chinook salmon spawn in the fall and steelhead trout in the spring, the species are different in size; chinook salmon tend to be larger because of earlier time of emergence. Similar patterns occur between juvenile coho and chinook salmon in British Columbia (Lister and Genoe 1970). In small Alaskan streams, selective segregation results in habitat partitioning between juvenile coho salmon and Dolly Varden (Dolloff and Reeves 1990). Each species occupies similar habitats when alone and in the presence of the other species. Coho salmon occupy mid-water positions that are defended from other fish. Dolly Varden are more closely associated with the stream bottom and are seldom territorial. Differences in life history features, such as those outlined above, as well as differences in morphology, behavior, and physiology that lead to selective segregation, are genetically encoded over time (Nilsson 1967).

## Human Impacts on Fish

The structure and composition of many native fish communities are modified by anthropogenic activities throughout the vast majority of Pacific coastal ecoregion. Several species of native fishes are extinct and many others are in need of special management considerations because of low or declining numbers (Williams et al. 1989, Nehlsen et al. 1991, Frissell 1993). More than 314 stocks of Pacific salmon are considered at moderate to high risk of extinction in coastal Washington, Oregon, and northern California (Forest Ecosystem Management Assessment Team 1993). In the same area, several resident fish, including bull trout (*Salvelinus confluentus*), Oregon chub (*Oregonichthys crameri*), and Olympic mudminnow (*Novumbra hubbsi*) are considered at risk because of low or declining populations (Williams et al. 1989). Slaney et al. (1996) found that more than 700 stocks of anadromous salmonids in British Columbia and the Yukon have a moderate to high risk of extinction. An additional 230 need special management consideration and 142 are already extinct. These stocks represent about 10% of the total estimated number of stocks

found in that area. Habitat alteration and introduction of nonnative fishes are the most frequently cited factors associated with the losses and declines (Li et al. 1987, Hicks et al. 1991, Bisson et al. 1992).

Physical habitats in rivers of all sizes throughout the Pacific coastal ecoregion have been simplified by human activities (Hicks et al. 1991). Large river systems (e.g., the Willamette River in Oregon) have been extensively channelized and diked for flood control and transportation (Figure 9.11) (Sedell and Froggatt 1984). Consequently, secondary channels, backwaters, and oxbows, which are important habitats for many juvenile fishes have been lost. McIntosh et al. (1994) reported that large pools, which are important habitats for many species and age-classes of fish, declined more than 50% in larger streams in western Oregon and other parts of the Pacific Northwest in the last 50 years. Structural elements such as large wood and boulders, which create habitat and complexity, also have been reduced in many systems by various activities, including timber harvest, urbanization, agriculture, and livestock grazing (Bisson et al. 1992).

It is difficult to generalize about the response of fish communities to habitat alteration because responses vary with the individual situations. Some species may respond positively to environmental changes and others negatively. The result of this differential response is generally a decrease in diversity because of changes in relative evenness rather than loss of species richness. In the Willamette River, Oregon, channelization has contributed, in part, to the decline of Oregon chub because of loss of off-channel habitats (Li et al. 1987). However, other species such as prickly sculpin (*C. asper*), redbelt shiner, northern squawfish (*Ptychocheilus oregonensis*), and chiselmouth (*Arocheilus alutaceus*) have increased because of increased availability of food in and on rock revetments (Hjort et al. 1984, Li et al. 1987). The structure and composition of fish communities of a pristine and a channelized urban stream in the Puget Sound area of Washington were similar in terms of species richness but evenness was greater in the pristine stream (Scott et al. 1986) (Figure 9.12). Bisson and Sedell (1984) and Hicks (1990) noted similar

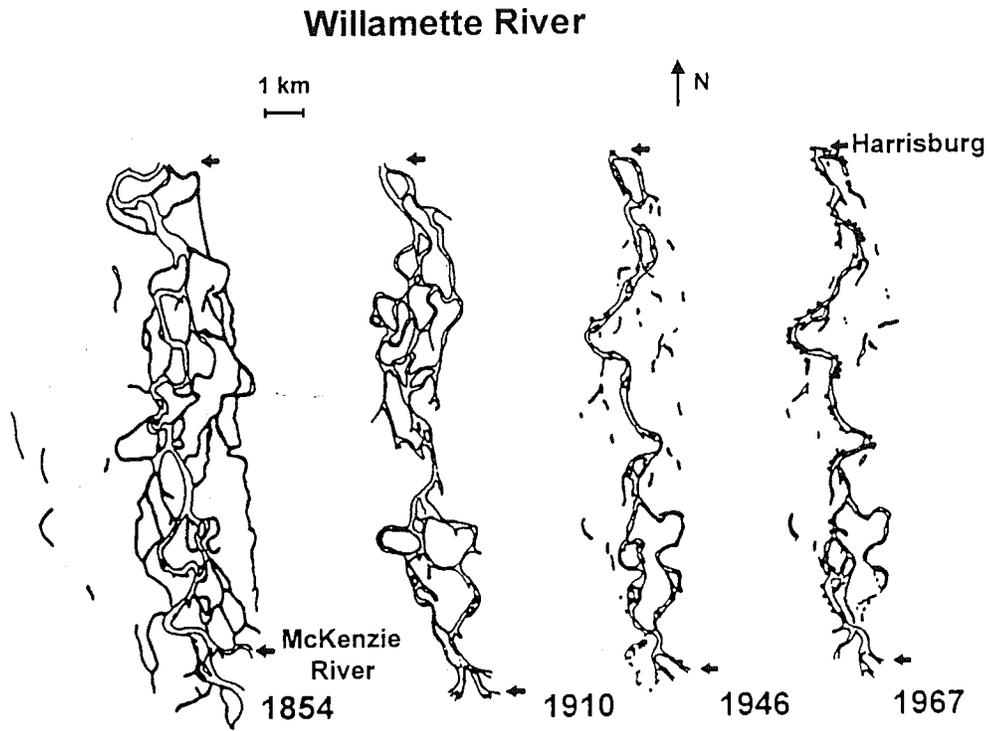


FIGURE 9.11. Changes in the floodplain and channel of the Willamette River, Oregon over 113 years as a result of channelization and diking (from Sedell and Froggatt 1984 with permission).

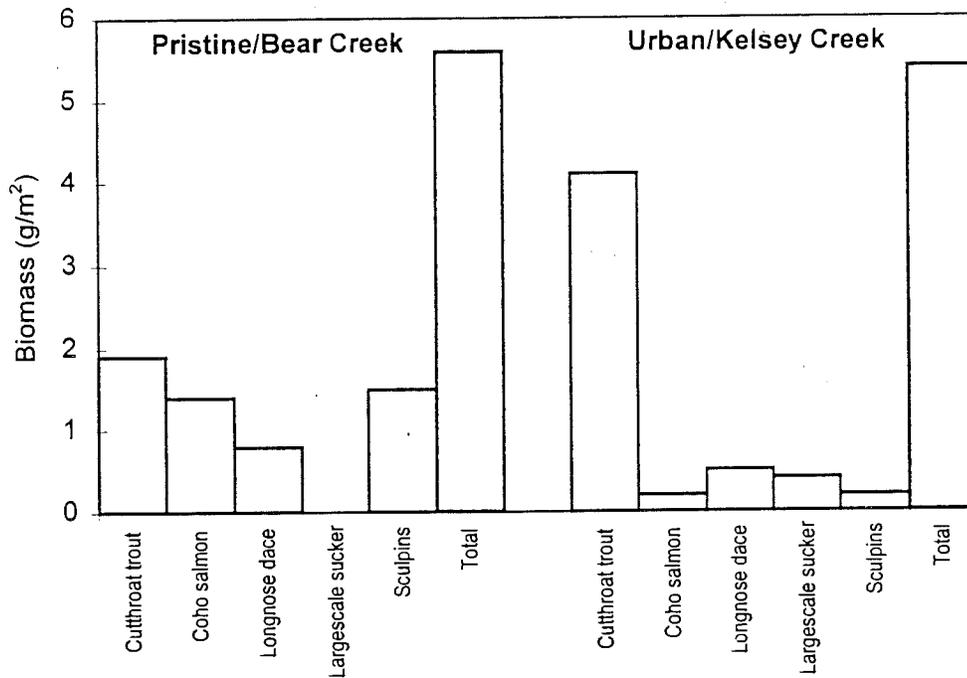


FIGURE 9.12. Composition of fish communities in a pristine stream (Bear Creek) and an urban stream (Kelsey Creek), Puget Sound, Washington (from Scott et al. 1986 with permission).

responses in communities of juvenile anadromous salmonids in streams in Washington and Oregon, respectively, that had been impacted by timber harvest. The diversity of assemblages of juvenile salmonids in coastal Oregon streams was greater in streams where less than 25% of the basin was subjected to timber harvest and associated activities compared to streams where more than 25% of the basin was harvested (Reeves et al. 1993). Again, the decrease in diversity resulted from changes in relative abundance rather than loss of species. Coho salmon generally increased in number whereas cutthroat trout declined. Similar responses to timber harvest have been observed in British Columbia (Hartman 1988, Holtby 1988, Scrivener and Brownlee 1989) and Oklahoma (Rutherford et al. 1987).

### Differential Response of Species

Changes in community diversity resulting from the differential response to alterations just described are a consequence of specific environmental changes. For example, water temperatures mediate competitive interactions between redbside shiner and juvenile steelhead trout (Reeves et al. 1987). At temperatures of 19 to 22°C, shiners displaced trout through exploitative competition (i.e., more efficiently obtaining food), whereas, trout are dominant at temperatures of 12–15°C because of interference competition (i.e., preventing access to food by defending territories). Dambacher (1991) attributed the distribution pattern of trout and shiners in Steamboat Creek, Oregon, to the changes in competitive interactions associated with changes in water temperature and reach gradient. Shiners dominate in low gradient, warm reaches, and steelhead dominate in cool reaches and warm reaches with high gradients. Water temperature mediates interactions for space and food between shiners and juvenile chinook salmon in the Wenatchee River, Washington (Hillman 1991) as well as competition for space between the riffle sculpin (*C. gulosus*) and the speckled dace in a California stream (Baltz et al. 1982).

Alteration of environmental conditions may reduce habitat suitability for some species but

increases it for others. Though freshwater fish exist over a wide range of conditions, a narrow range is generally most favorable for a species (Larkin 1956). Relative abundances of the species in the community shift when conditions change; those favored by the new conditions increase and vice versa. This pattern prevails in juvenile anadromous salmonid assemblages in streams in coastal Oregon altered as a result of timber harvest activities (Reeves et al. 1993). Numbers of coho salmon decline in steeper gradient systems but numbers of trout (age 1+) decline in lower gradient systems. Loss of structure (primarily large woody debris) in higher-gradient streams results in the loss of slow-water habitat which is favorable to coho salmon. Coho salmon are better suited to slow water because their bodies are dorsally-ventrally compressed and their relatively large fins allow better maneuverability. Lack of pools and high-velocity areas associated with large woody debris in lower-gradient streams results in conditions less suitable to trout, particularly cutthroat. Trout are more cylindrical and thus, better suited for fast water (Bisson et al. 1988). Rutherford et al. (1987) attributed changes in fish communities in Oklahoma streams altered by timber harvest to the tolerance of species for environmental extremes; more tolerant species were able to maintain themselves better than less tolerant species.

Many exotic fishes (i.e., nonnative) have become established in many river systems in the Pacific coastal ecoregion as a result of changes in environmental conditions associated with anthropogenic activities. Consequently, some native communities have been altered as a result of competition with, or predation from, various exotic species. In the Columbia River, for instance, dams increase water temperatures, create large areas of slow water, and decrease the amount of riverine environment. Before the introduction (intentional and accidental) of exotic species, native predators (e.g., burbot [*Lota lota*], bull trout, cutthroat trout), which all have small mouths, foraged primarily on smaller fish species and age-classes (Figure 9.13a) (Li et al. 1987). Many exotic predators (e.g., smallmouth bass [*Micropterus dolomieu*], channel catfish [*Italusus*]) have larger jaws and

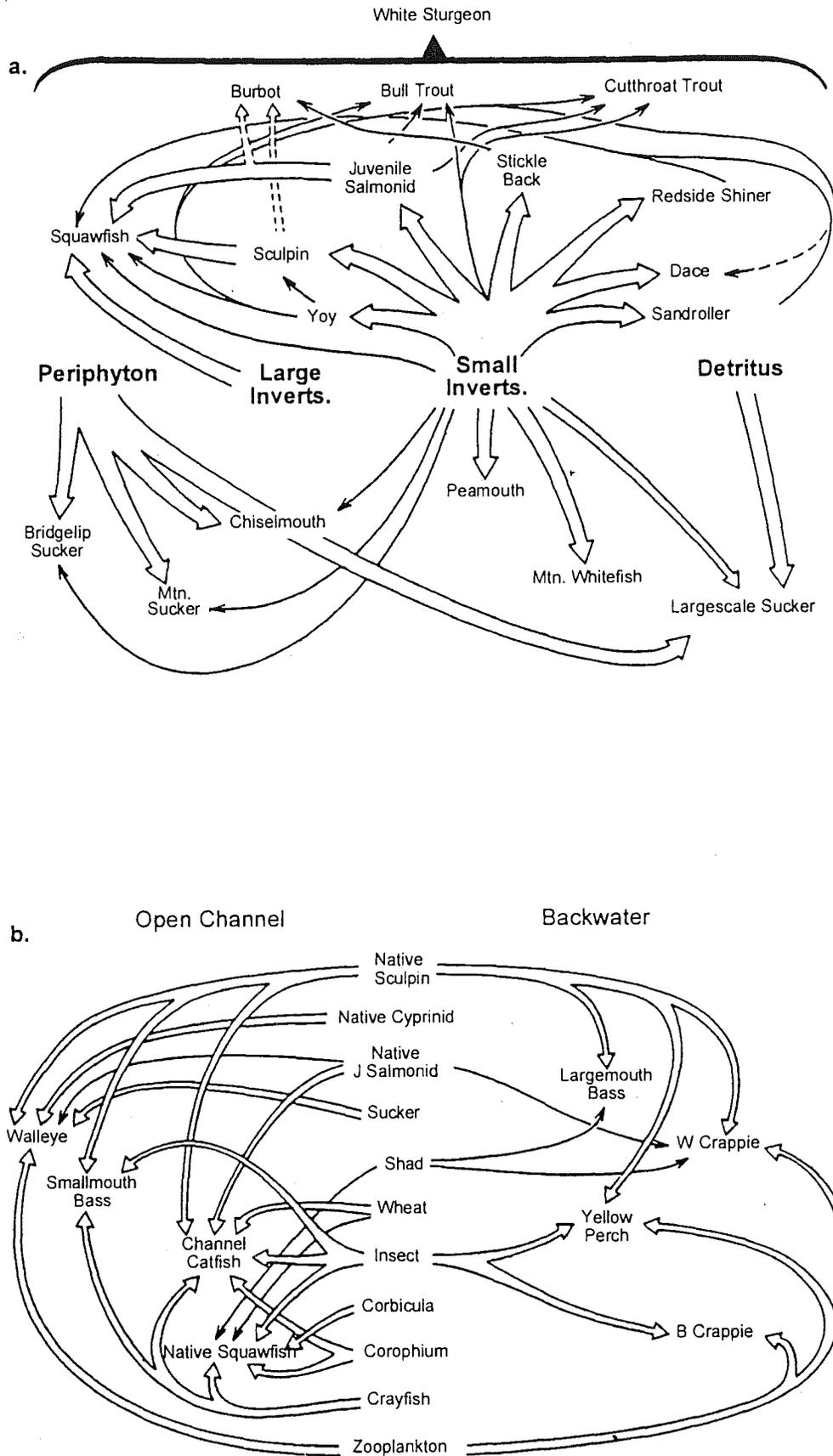


FIGURE 9.13. Hypothetical food webs of the middle and lower Columbia River (a) before 1800 and (b) following major changes resulting from human

activity, ca. 1888–1983 (from Li et al. 1987 © University of Oklahoma Press with permission).

prey on larger individuals previously not affected by native predators. Also, unlike native predators, some exotic predators such as walleye (*Stizostedion vitreum*) are schooling nocturnal predators. Native salmonids (primarily smolts or immature individuals moving to the ocean) migrate at night to avoid predation by native fishes. However, walleye and other exotic fishes are efficient nocturnal feeders thereby reducing many native fish populations (Wydoski and Whitney 1979, Maule and Horton 1984) while becoming dominant components of the community (Figure 9.13b).

Competition with introduced species also causes a decline in native fishes. Wide-scale introduction of brook trout (*S. fontinalis*) has been implicated in the decline of native bull trout (Ratliff and Howell 1992). Brook trout and bull trout use similar food (Wallis 1948) and habitat (Dambacher et al. 1992) but brook trout reproduce at an earlier age and can numerically overwhelm bull trout. They also reduce the reproductive capacity of bull trout through hybridization (Leary et al. 1993). In addition, interactions with introduced competitors and predators, in conjunction with habitat loss and alteration, has contributed to the decline of Oregon chub in the Willamette River, Oregon (Pearsons 1989).

## Disturbance

Disturbance strongly influences the structure and composition of biotic communities (Krebs 1994). Periodic disturbance creates conditions that allow some species to persist and that prevent competitively superior species from dominating communities, particularly at local scales (such as reaches or habitat units). The response of communities to disturbance depends, among other things, on the duration, intensity, and frequency of the disturbance. Yount and Neimi (1990) modified the definition of disturbance established by Bender et al. (1984) as "press" or "pulse." A *pulse disturbance*, such as flood or wildfire in an undisturbed system, allows an ecosystem to remain within a normal range of conditions or domains and to recover conditions that were present prior to disturbance. A *press disturbance* forces an ecosystem to a dif-

ferent set of conditions or domains. Yount and Neimi (1990) considered many anthropogenic activities to be press disturbances, for example, the construction of dams on the Columbia River. Dams alter the system from flowing to standing water and reduce variation in flow below the dams. These and other changes caused by dams have resulted in pronounced changes in the structure and composition of the fish community (Figure 9.13a and 9.13b) (Li et al. 1987). Many stream biota cannot recover from the effects of anthropogenic disturbances because, lacking an analogue in the natural disturbance regime, they may not have evolved the appropriate characteristics for recovery (Gurtz and Wallace 1984). Changes in environmental conditions are often too drastic and rapid for native fishes to adapt.

Modification of the type, frequency, or magnitude of natural disturbances alters fish communities (White and Pickett 1985, Hobbs and Huenneke 1992). Changes in the disturbance regime are manifested in extirpation of some species, increases in species favored by postdisturbance habitats, and invasion of exotics (Levin 1974, Harrison and Quinn 1989, Hansen and Urban 1992). Alteration of annual flooding on the Colorado River has contributed to the loss of many habitats and environmental conditions, and ultimately the decline of many unique native fishes (Tyus 1987, 1991). Additionally, dam construction has altered water temperatures. Spring water temperatures are lower because colder water is released from the bottom of the reservoirs. The effect is reduced reproductive success and decline of such native species as the razorback sucker (*Xyrauchen texanus*).

Streams throughout the Pacific coastal ecoregion operate differently from natural systems because of human disturbances (Li et al. 1987). Yet, the response of native fish communities in the Pacific coastal ecoregion to alteration of disturbance regimes, perhaps with the exception of those impacted by large dams, is poorly understood or appreciated at present. Nonetheless, the alteration of natural disturbance regimes has contributed to the widespread decline of anadromous salmonids (Reeves et al. 1995). Landscapes in the Pacific

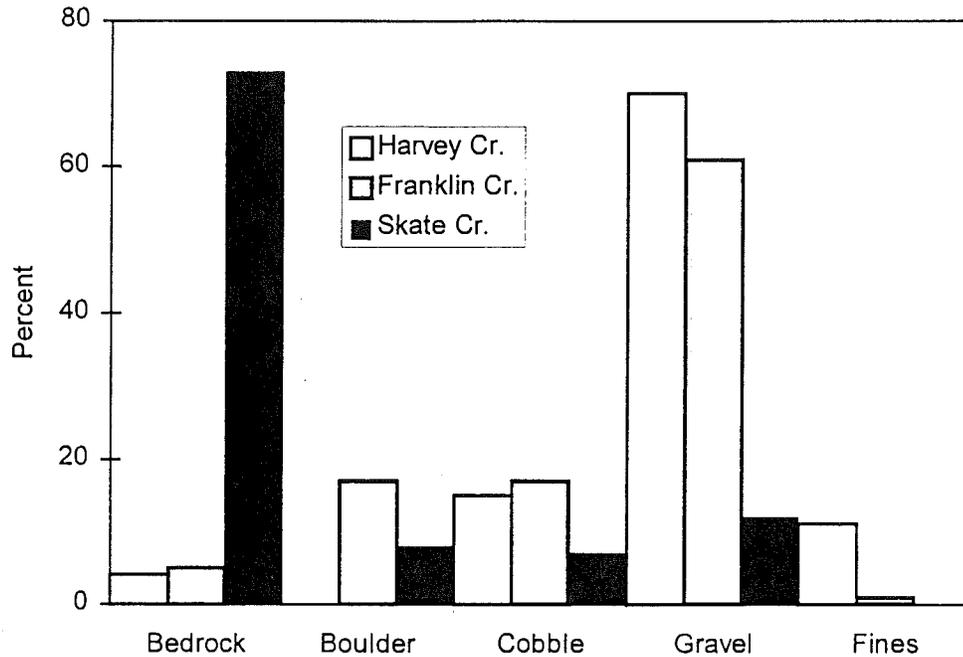


FIGURE 9.14. Substrate composition in three streams of the central Oregon Coast Range at different times since the last major natural disturbance. Time since the last major natural disturbance was 90–100 years

for Harvey Creek, 160–180 years for Franklin Creek, and more than 3000 years for Skate Creek (from Reeves et al. 1995 with permission).

coastal ecoregion historically were dynamic in space and time (Naiman et al. 1992, Chapter 11). In the central coast of Oregon, for example, periodic catastrophic wildfire and hillslope failure occurred on average every 250 to 300 years (Benda 1994, Chapter 11) and were followed by periodic extirpations of local populations (Reeves et al. 1995). Over time, disturbed areas developed different conditions as a result of changes in the amount of sediment (Figure 9.14) and wood in the stream channel (Table 9.6). The landscape was a mosaic of habitat conditions in streams, similar to varia-

tion in successional states observed in terrestrial systems. The relative abundances of species changed over time (Table 9.6). Coho salmon were present at all times while trout were most abundant at intermediate times (160–180 yrs) from disturbance, when habitat conditions were most diverse.

Anadromous salmonids have evolved strategies (e.g., straying of adults and high fecundity) to persist in the dynamic landscapes and streams systems of the Pacific coastal ecoregion (Naiman et al. 1992, Reeves et al. 1995). Straying adults (which are relatively fecund) as well

TABLE 9.6. Composition of juvenile anadromous salmonids and mean number of pieces of large wood (mean diameter >0.3 m and length >3 m) per 100 m in three streams in the central Oregon Coast Range at different times since last major natural disturbance.

Stream	Mean number of pieces of large wood/100m	Years since last major disturbance	Mean percent of estimated total numbers		
			Coho Salmon (Age 0)	Steelhead Trout (Age 1+)	Cutthroat Trout (Age 1+)
Harvey Creek	7.9	90–100	98.0	1.0	1.0
Franklin Creek	12.3	160–180	85.0	12.5	2.3
Skate Creek	23.5	>300	100.0	0.0	0.0

Modified from Reeves et al. 1995.

TABLE 9.7. Features of natural and human disturbance regimes.

	Natural disturbance	Human disturbance
Magnitude	High	Low-Moderate
Frequency	Low	High
Area Impacted	Small	Large
Degree to which Natural Processes Retained	Strong	Weak
Legacy of Disturbance	Complex	Simple

as moving juveniles can colonize newly disturbed areas. But human activities, such as timber harvest, agriculture, and urbanization, have altered the historical natural disturbance regime (Table 9.7). Affected landscapes are less heterogeneous than the natural systems and disturbed more frequently and over larger areas. As a result, the range and type of conditions in aquatic systems are much simpler and thus do not support the most diverse communities (Reeves et al. 1995).

The differential response of native fishes to anthropogenic disturbances and the increasing dominance of exotic species in Pacific coastal ecoregion rivers and streams suggests that press disturbances have become a major influence on fish communities and aquatic ecosystems. It is unlikely that native fish communities will recover unless the role of natural disturbance in structuring these communities is better regulated or mimicked (Reeves et al. 1995).

## Future Management Directions

Although managing for biodiversity is currently the objective of many management plans in the Pacific coastal ecoregion, it is not exactly clear what biodiversity means. Diversity has two components, species richness (i.e., numbers) and relative abundance (see Chapter 17 for more detail) and management plans for each component may be very different.

A focus on species richness without concern for relative abundance of other species results in development of conditions more favorable for the species of interest at the expense of

other species. Each species has a specific range of conditions over which it performs best (Larkin 1956). It is unlikely that this range overlaps exactly for any two species. Thus, creating optimal conditions for a particular species may result in conditions less favorable for other species. Consequently, what are perceived to be relatively small changes in environmental conditions can reduce the abundance of nontarget species and have significant effects on the structure and composition of stream fish communities. Focusing on relative abundance requires management plans which develop a range of conditions suitable for a suite of species. This may mean that maximum abundance or production of any particular species is not reached. Clearly, it is important to identify the type of diversity desired before developing management plans.

Until recently, habitat management decisions were premised on the belief that habitats could be manipulated with technology to benefit fish (Sedell et al. 1997). This perspective has changed, partly because of the awareness of the continued trends toward widespread habitat simplification. Management of fish communities has shifted towards an ecosystem approach (Frissell et al. 1997, Lichatowich 1997). Although the definition of ecosystem management is still evolving, aspects related to fish communities include consideration of natural disturbance regimes, landscape contexts, and temporal and spatial dimensions matched to the dynamics of native fish populations (Bisson et al. 1997). Integration of macro-scale physical and biological processes into a broader spatial and temporal ecosystem framework is necessary to explain the dynamics of stream fish communities (Power et al. 1988) and to recover and maintain native fish communities in the Pacific coastal ecoregion.

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Editors

# River Ecology and Management

Lessons from the  
Pacific Coastal  
Ecoregion

Sylvia Kantor  
Associate and Managing Editor

With 202 Illustrations



Springer

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Seattle, WA 98195  
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Robert E. Bilby  
Weyerhaeuser Company  
Tacoma, WA 98477  
USA

*Cover:* Queets River, Olympic National Park, Washington (Photo by Tim Hyatt)

Library of Congress Cataloging-in-Publication Data  
River ecology and management: lessons from the Pacific coastal  
ecoregion / [edited-by] Robert J. Naiman, Robert E. Bilby.

p. cm.

Includes index.

ISBN 0-387-98323-6 (hc: alk. paper)

1. Stream ecology—Pacific Coast Region (North America) 2. Stream  
conservation—Pacific Coast Region (North America) I. Naiman,

Robert J. II. Bilby, Robert E.

QH104.5.P32R57 1998

577.6'4'0979—dc21

97-44766

Printed on acid-free paper.

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Production coordinated by Chernow Editorial Services, Inc., and managed by Terry V. Kornak; manufacturing supervised by Joe Quatela.

Typeset by Best-set Typesetter Ltd., Hong Kong.

Printed and bound by Braun-Brumfield, Inc., Ann Arbor, MI.

Printed in the United States of America.

9 8 7 6 5 4 3 2 1

ISBN 0-387-98323-6 Springer-Verlag New York Berlin Heidelberg SPIN 10523806