

Coevolution of the Pacific salmon and Pacific Rim topography

David R. Montgomery

Department of Geological Sciences, University of Washington, Seattle, Washington 98195, USA

ABSTRACT

The late Cenozoic radiation of the Pacific salmon and trout (*Oncorhynchus* spp.) resulted in five species that are widely distributed in western North America and occupy distinct parts of river networks. The dramatic radiation of the Pacific salmon contrasts with the history of the Atlantic salmon, which have evolved little since the divergence of *Oncorhynchus*. Conventional hypotheses for the radiation of the Pacific salmon stress geographic isolation due to Pleistocene glaciations, but paleontological evidence dates their speciation to the middle Miocene to early Pliocene. Tertiary marine cooling may have spurred the development of anadromy in salmon and other fish, but does not readily explain the different evolutionary trajectories for the Pacific and Atlantic salmon. The timing of Pacific salmon speciation corresponds to significant physiographic changes around the Pacific Rim, suggesting that increased topographic diversity due to an active tectonic regime contributed to the evolution of the Pacific salmon.

Keywords: geomorphology, uplift, salmon, evolution, biogeography.

INTRODUCTION

The recent listing of runs of chinook (*Oncorhynchus tshawytscha*) and coho salmon (*O. kisutch*) as endangered species in California, Oregon, and Washington has focused attention on the adaptation of fish populations to the dynamic nature of mountain environments (Lichatowich, 1999). In particular, the need to address the ecological context within which to define and manage evolutionarily significant units under the Endangered Species Act (Waples, 1991) motivates efforts to understand the process link between landscape dynamics and fish populations. Although such understanding provides context important for designing and assessing recovery plans for the various species of salmon, the fundamental question remains as to why there are five species of Pacific salmon (*O. spp.*) in western North America, but only one species of Atlantic salmon (*Salmo salar*) in eastern North America. Here I explore the hypotheses that the evolution of the Pacific salmon reflects local geographic isolation caused by the Miocene-Pliocene rise of coastal mountains and/or radiation into a more variable environment created by physiographic changes driven by regional tectonics.

EVOLUTION OF THE SALMON

The phylogeny proposed by Stearley (1992) shows that the Pacific salmonids diverged into five species of salmon and at least five species of trout in North America since the common ancestor they shared with the Atlantic salmon (Fig. 1). Devlin (1993) used sequence differences in genes from Atlantic salmon, rainbow trout (*O. mykiss*), and sockeye salmon (*O. nerka*) to estimate that *Salmo* and *Oncorhynchus* diverged ca. 20 Ma. Similarly, Behnke (1992) placed the separation of *Salmo* and *Oncorhynchus* as occurring by 15 Ma. Stearley (1992) argued that Miocene cooling of the Arctic Ocean isolated the

Atlantic and Pacific populations, thereby leading to their divergence.

But what led to the striking difference in subsequent evolutionary trajectories for salmon on the east and west coasts of North America? Conventional hypotheses for the controls on differentiation of Pacific salmon and trout invoke advance and retreat of Pleistocene glaciers as the pump for isolation, diversification, or behavioral modification of various species and stocks (Neave, 1958; Lichatowich, 1999). However, Pleistocene glaciation affected both coasts of North America, and it is unclear why an evolutionary response to glaciation would have been restricted to the west coast. In addition, genetic analyses of mitochondrial DNA show that the modern species of Pacific salmon evolved before the ca. 2 Ma onset of Pleistocene glaciation (Thomas et al., 1986).

The fossil record of salmon is fragmentary, but accumulating fossil evidence indicates that most of the differentiation leading to the modern species occurred long before the Pleistocene (Stearley, 1992). The earliest fossil of the Salmonidae is the Eocene *Eosalmo driftwoodensis* from British Columbia (Wilson and Williams, 1992). Although there is a substantial gap in the fossil record, *Salmo* and *Oncorhynchus* apparently diverged by the early Miocene (McPhail,

1997). By 6 Ma, species resembling the modern sockeye, pink (*O. gorbuscha*), and chum (*O. keta*) salmon were present in Idaho and Oregon (Smith, 1992). In addition, rainbow trout, cutthroat trout (*O. clarki*), and Pacific salmon had diverged by the beginning of the Pliocene (Stearley and Smith, 1993). The most recent divergence according to the phylogeny proposed by Stearley (1992)—that of the pink and sockeye salmon—also had occurred by 6 Ma (Smith, 1992). Hence, the fossil record establishes that speciation of the five distinct species of Pacific salmon occurred between 20 and 6 Ma.

Differences in resource availability between terrestrial and marine environments have been interpreted as the cause of the development of anadromy in general (Gross et al., 1988), and Stearley (1992) considered that global Oligocene-Miocene cooling contributed to development of diadromy in salmonids. Hence, one might hypothesize that speciation of the Pacific salmon developed to take advantage of greater marine productivity. The marine oxygen isotope record (Miller et al., 1987) indicates an extended cooling from the Eocene to Oligocene followed by a period of relative climate stability until a less pronounced cooling ca. 15 Ma and another major episode in the Pliocene-Pleistocene (Fig. 2). Although marine cooling provides a compelling explanation for the development of anadromy in both the Atlantic and Pacific salmon, the period during which the Pacific salmon radiated (20–6 Ma) corresponds to the weakest of the three Tertiary cooling episodes. Furthermore, global marine cooling does not explain why the Pacific salmon radiated but the Atlantic salmon did not.

Dimmick et al. (1999) analyzed the phylogeny and biogeography of *Oncorhynchus* by using Lynch's (1989) method of quantifying biogeographic overlap to gauge allopatric versus sympatric speciation—the degree to which geographic

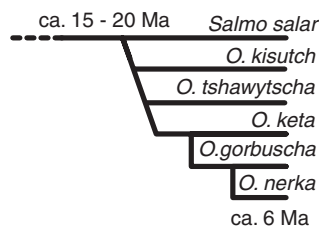


Figure 1. Phylogeny of Pacific salmon proposed by Stearley (1992) showing timing of geologic constraints.

isolation and environmental change, respectively, influenced speciation. They found that within *Oncorhynchus*, the various species of trout generally exhibited strong evidence of allopatry, but that the Pacific salmon exhibited strong evidence of sympatric speciation (Dimmick et al., 1999). Despite their similar biogeographic ranges, the five North American species of Pacific salmon use different habitats within a watershed. Pink and chum salmon generally spawn in the lower stream reaches in a watershed, sockeye salmon spawn in lakes, coho salmon spawn in smaller tributaries, and chinook salmon spawn in the main stem and larger tributaries (Lichatowich, 1999; Montgomery et al., 1999). The general spatial segregation of Pacific salmon habitat suggests that evolution of the Pacific salmon selected for survival in distinct parts of mountain drainage basins (Lichatowich, 1999). Although it is difficult to argue for a marine control on this terrestrial geographic segregation, the strikingly different evolutionary trajectories for the Atlantic and Pacific salmon parallel differences in the Cenozoic evolution of North American topography.

EVOLUTION OF EAST COAST TOPOGRAPHY

The evolution of the topography of the eastern coast of the United States is dominated by the history of the Appalachian range. The orogenic activity that produced the Appalachians occurred in several phases from the Ordovician to the Triassic (Rodgers, 1970; Judson, 1975). This series of Paleozoic orogenies ended after the Jurassic when rifting stopped and the Appalachian system came under a regime of compressive stress that has continued to the present (Pavich, 1985). The Appalachians approached their current form in the Late Jurassic or Cretaceous, and many contemporary features can be recognized on reconstructions of the early Miocene landscape (Cleaves, 1989). General physiographic stability of the Appalachian Piedmont can be inferred from an approximately steady-state interplay of weathering, erosion, and isostatic uplift for about the past 70 m.y. (Pavich, 1985). Although there is some evidence of Cenozoic tectonic activity, and glacial episodes influenced the region, the post-Cretaceous evolution of the eastern seaboard has been dominated by changes in sea level (Hack, 1969; Pazzaglia, 1993).

EVOLUTION OF PACIFIC RIM TOPOGRAPHY

In contrast to the stability of eastern North America, the physiography of the western seaboard has changed significantly in the late Cenozoic. Cole and Armentrout (1979) reviewed the Neogene paleogeography of the western United States and concluded that middle Miocene tectonic change fragmented broad, long-lived paleogeographic patterns and led to uplift along the entire west coast. Although the mean elevation of

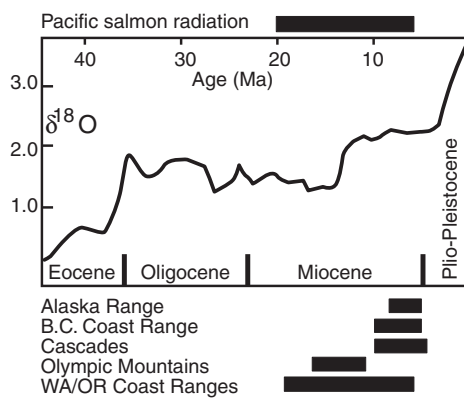


Figure 2. Relationship of radiation of Pacific salmon (top bar) to Miller et al.'s (1987) marine oxygen isotope curve and onset of uplift on Pacific Rim of North America (bottom bars). B.C.—British Columbia; WA/OR—Washington/Oregon.

the Cordilleran interior has been declining since Basin and Range extension began to break up a high plateau ca. 16 Ma (McKee, 1971; Wernicke et al., 1987; Wolfe et al., 1997; Chase et al., 1998), regional extension driven from the east could have resulted in uplift of the coastal ranges. The specific uplift history of the Pacific Coast Ranges (summarized in the following sections and Fig. 2) and possible relationships to Basin and Range extension will continue to be debated, but it is apparent that substantial physiographic changes occurred from the middle Miocene to early Pliocene throughout the present North American range of *Oncorhynchus*.

Alaska Range

The onset of surface uplift in the central Alaska Range is constrained by sedimentological and paleocurrent data to the east of Denali near the Nenana River. There, Miocene sediments contain detritus from the Brooks Range to the north, lack detritus of central Alaskan provenance, and have paleocurrent directions to the south—across the current central Alaska Range (Wahrhaftig et al., 1969). Fitzgerald et al. (1993) used these data to infer Miocene elevations throughout the current range that were comparable to the low-relief, 300-m-high tundra and outwash plains on its modern flanks. The Miocene strata are overlain by the Grubstake Formation; bimodal paleocurrents flowing to the north and south appear between an 8 Ma ash bed and the overlying Pliocene Nenana Gravels (Wahrhaftig et al., 1969). Surface uplift of the central Alaska Range therefore commenced between 8 Ma and the Pliocene deposition of the Nenana Gravels.

British Columbia Coast Range

The present high elevation and differential uplift of Miocene basalt erupted onto low-relief surfaces point to substantial post-Miocene uplift of the British Columbia Coast Range (Douglas

et al., 1970; Parrish, 1983). Fission-track dating of zircon and apatite from throughout the British Columbia Coast Range shows slow rock uplift from 30 to 15 Ma and significant acceleration in the late Miocene (Parrish, 1983). In addition, Harrison et al. (1979) inferred a period of isostatic stability from 45 to 10 Ma followed by regional uplift beginning ca. 10 Ma on the basis of fission-track, K-Ar, and Rb-Sr mineral dating of plutons in the British Columbia Coast Range. Basalts dated as 10–6 Ma filled valleys of the ancestral Fraser River and covered large areas of low relief along the eastern flank of the Coast Range (Rouse and Mathews, 1979). Paleoenvironmental reconstructions on the eastern side of the British Columbia Coast Range indicate no significant topographic barrier prior to the late Miocene and a sharp climate deterioration in the late Miocene, which in combination with an extensive nondepositional interval imply substantial post-Miocene surface uplift (Rouse and Mathews, 1979).

Cascade Range

Chaney (1938) noted that the Cascades today separate widely different environments because of a rain shadow effect, and that the Eocene forests of interior Oregon were closely related to coastal forests. He therefore concluded that the Eocene Cascade Range was not a high topographic barrier. The area now occupied by the Cascades was covered by peat bogs and deltaic lowlands in the Eocene, and Oligocene sediments indicate that the site of the present range was a low-relief plain (Weaver, 1937; Mackin and Cary, 1965). The early Pliocene Dalles and Troutdale floras, which are on opposite sides of the Cascades, represent widely different climatic conditions; Chaney (1944) interpreted this to indicate that the Cascades presented a substantial topographic barrier by the early Pliocene. Uplift of the Cascade Range postdates the eruption of the Columbia flood basalts that covered much of southern Washington in the Miocene (Mackin and Cary, 1965). On the basis of elevation differences of the Columbia flood basalts and the age of the Ellensburg Formation and the Simcoe Basalt, Hammond (1979) argued for >1.5 km of uplift in the northern Cascades beginning ca. 10–5 Ma.

Olympic Mountains

The emergence of the Olympic Mountains is indicated by a regional unconformity beneath the Miocene Montesano Formation and by sedimentological evidence for onset of the unroofing of the Olympic subduction complex. The regional unconformity is bracketed stratigraphically by two units of the Columbia River basalts dated as 17–12 Ma (Brandon et al., 1998). The late Miocene Montesano Formation contains the first inclusion of material derived from unroofing of the Olympic subduction complex (Brandon and Calderwood, 1990). Extensive fission-track dat-

ing of samples derived from a wide range of elevations in the Olympic Mountains shows that accelerated rock uplift began to raise the range ca. 17–12 Ma (Brandon et al., 1998).

Washington and Oregon Coast Ranges

During the Eocene, the western Washington Coast Range consisted of a coastal plain (Weaver, 1937). The Eocene Tyee Formation, which composes much of the Oregon Coast Range, was deposited in a deltaic environment on a narrow continental shelf (Dott and Bird, 1979). A regional Miocene unconformity has long been recognized in the coastal ranges of Washington and Oregon, and by the late Miocene western Washington was elevated above sea level (Cole and Armentrout, 1979).

California Coast Ranges and Sierra Nevada

The California Coast Ranges have a complex uplift history that reflects the combined influence of thermal upwelling associated with passage of the Mendocino triple junction (Zandt and Furlong, 1982), local effects of transverse deformation through restraining fault bends (Anderson, 1990), and margin-wide compressional deformation (Aydin and Page, 1984). The general rise of the Coast Ranges began in the middle to late Pliocene, but stratigraphic evidence demonstrates that some areas of the Coast Ranges were emergent in the Miocene to early Pliocene (Page, 1981). The timing of surface uplift of the Sierra Nevada remains controversial. Classic studies argued for substantial Miocene-Pliocene uplift (Axelrod, 1957; Huber, 1981), but recent work supports the interpretation of no substantial surface uplift since the early Tertiary (House et al., 1998; Chamberlain and Poage, 2000).

DISCUSSION

The major divergences within *Oncorhynchus* that gave rise to the Pacific salmon occurred between 20 Ma and 6 Ma, long before Pleistocene glaciation and well after the onset of Tertiary climate deterioration, but coincident with the late Miocene reorganization of the topography of the Pacific Rim of North America. While it is not clear where in their current range across the north Pacific that Pacific Salmon speciated, their entire range spans tectonically active continental margins. Due to the sparse fossil record of freshwater fish, the location(s) of salmon speciation may never be definitively established. However, the hypothesis that they coevolved with the regional topography offers an explanation for the different evolutionary trajectories of the Pacific and Atlantic salmon.

What was the mechanism by which topographic change could have triggered salmon evolution? The late Tertiary changes in climate and topography in western North America opened new ecozones that plants and animals from prior environments invaded and in which they continued to evolve (Axelrod, 1957). Geographic isola-

tion due to drainage-basin reorganization in the wake of Basin and Range extension is recognized as contributing to trout speciation (Smith, 1981; Behnke, 1992). Similarly, the uplift of coastal ranges would have bifurcated coastal rivers and thereby resulted in the potential for isolation of local salmon populations. However, a mechanism for salmon speciation more in line with Dimmick et al.'s (1999) interpretation of sympatric speciation is that topographic changes along the coast and in inland watersheds would have created a more varied suite of stream types that today host different salmonids (Montgomery et al., 1999).

Most salmon return to their natal stream to spawn, although straying behavior is important for recolonization of streams after disturbances. Kendall and Behnke (1983, p. 142) argued that salmonids "tend to form genetically isolated populations," in part due to their "precise homing ability," and further noted that salmonids "seem to be able to occupy new niches and habitats as these become available." Channel processes and disturbance regimes vary among different types of channels (Montgomery and Buffington, 1998) and heritable adaptations in run timing or behavior could have started to isolate fish using different reaches into distinct populations. With relatively low straying behavior, strongly heritable traits, and the potential for strong selection in new environments due to fundamental differences in channel processes, an increased range of stream types could provide a mechanism for sympatric speciation.

The general timing of major physiographic change on the Pacific Rim coincides with the radiation of the Pacific salmon, suggesting that the salmon and topography of western North America coevolved in response to tectonic forcing. Other explanations that have been offered for evolution of the Pacific salmon fail to explain basic aspects of their radiation. A glacial driver cannot explain why the various species of Pacific salmon existed before the Pleistocene, even though glaciations may have influenced the subsequent distribution and diversification of populations and stocks. Similarly, an oceanic cause does not satisfactorily explain the differences in evolutionary history between the Atlantic and Pacific salmon. A tectonic origin of the radiation of the Pacific salmon is not incompatible with these other processes having influenced salmon evolution—it is likely that local isolation due to glacial advances helped to diversify and differentiate different stocks of salmon, and the climate influence is apparent in the evolution of anadromy in both the Pacific and Atlantic salmon. However, the proposed tectonic driver for the radiation of *Oncorhynchus* could explain the different evolutionary trajectories of the Atlantic and Pacific salmon. If the hypothesized mechanism of Pacific salmon radiation into more diverse aquatic habitats is correct, then the Pacific salmon pro-

vide an example of how changes in geologic processes may promote speciation through increased topographic diversity.

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