2008

Evolutionary history of Pacific salmon in dynamic environments

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SYNTHESIS

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Abstract

Contemporary evolution of Pacific salmon (*Oncorhynchus* spp.) is best viewed in the context of the evolutionary history of the species and the dynamic ecosystems they inhabit. Speciation was complete by the late Miocene, leaving *c.* six million years for intraspecific diversification. Following the most recent glacial maximum, large areas became available for recolonization. Current intraspecific diversity is thus the product of recent evolution overlaid onto divergent historical lineages forged during recurrent episodes of Pleistocene glaciation. In northwestern North America, dominant habitat features have been relatively stable for the past 5000 years, but salmon ecosystems remain dynamic because of disturbance regimes (volcanic eruptions, landslides, wildfires, floods, variations in marine and freshwater productivity) that occur on a variety of temporal and spatial scales. These disturbances both create selective pressures for adaptive responses by salmon and inhibit long-term divergence by periodically extirpating local populations and creating episodic dispersal events that erode emerging differences. Recent anthropogenic changes are replicated pervasively across the landscape and interrupt processes that allow natural habitat recovery. If anthropogenic changes can be shaped to produce disturbance regimes that more closely mimic (in both space and time) those under which the species evolved, Pacific salmon should be well-equipped to deal with future challenges, just as they have throughout their evolutionary history.

Introduction

Both Pacific salmon* (*Oncorhynchus* spp.) and Atlantic salmon (*Salmo salar*) have experienced wide-spread population declines and extirpations (Jonsson et al. 1999; Gustafson et al. 2007), and both are strongly affected by anthropogenic changes to the freshwater and marine ecosystems they inhabit. These changes alter selective regimes the salmon experience and can be expected to elicit an evolutionary response – a phenomenon considered by many of the papers in this special issue. A fuller understanding of the nature and extent of these evolutionary changes can best be achieved in the context of the evolutionary history of salmon and the dynamic environments

*In this paper we consider steelhead (anadromous form of *Oncorhynchus mykiss*) to be honorary Pacific salmon.

in which they evolved. The historical template describing the tempo and mode of dynamic changes to Pacific salmon habitats can be particularly useful in assessing likely consequences of future anthropogenic changes. In general, salmon populations should have sufficient evolutionary capital to respond to changes that fall within the historic temporal and spatial scales of natural disturbance regimes, but larger changes might require an evolutionary response that is outside the range of what salmon can muster.

In this paper, we attempt a synthesis of some of the major features of Pacific salmon evolution, with particular emphasis on the interplay between variable environments and the evolutionary responses by salmon populations. Because rates of phenotypic change (and perhaps evolutionary change) are higher in human-altered landscapes (Hendry et al. 2008), we also consider how anthropogenic changes affect contemporary evolution of salmon. We

illustrate with examples drawn primarily from Puget Sound and the interior Columbia River basin – areas in the northwestern United States that have two attractive features for our analyses. First, these areas were at or near the southern extent of continental glaciation in the Pleistocene, so they have a rich and dynamic geologic history. Second, in both areas the biological attributes of the populations are well characterized and detailed information about historical ecological/environmental conditions is available, which facilitates joint analysis of biological and physical processes.

Ancestral traits and speciation: the Miocene and before

Whether ancestors of salmon were of freshwater or marine origin is open to debate (McDowall 2002; Hendry and Stearns 2004; Quinn 2005). More germane to our purposes is the propensity with which anadromous forms adopt a freshwater life history, and vice versa. We briefly consider this topic later (see Synthesis and discussion).

As a result of an autotetraploid event an estimated 65–95 million years ago (MA), fishes of the family

Salmonidae have about twice as many chromosome arms and twice the DNA content as closely related species (Allendorf and Thorgaard 1984; Ramsden et al. 2003). Duplicated genes can evolve rapidly because the presence of another 'normal' gene provides evolutionary flexibility. It seems likely that tetraploidy might provide a buffer against inbreeding depression (making it easier for small, isolated populations to persist); in contrast, we expect that the duplicated array of chromosomes might complicate meiosis and make outbreeding depression more likely. However, we are not aware of empirical evidence that speaks to these points.

The geologic history of the Pacific Northwest prior to the Pliocene was dominated by accretion of new terranes, volcanism, and upliftment of major mountain ranges such as the Cascades (Fig. 1). From about 37–57 MA, the region that is now the Washington Cascades was a broad coastal plain. Massive basalt eruptions between 6 and 17 MA flowed across the central Columbia River basin to the Pacific Ocean (Hooper 1997). Upliftment of the Cascade, Olympic, and Coast Ranges did not begin until 8–15 MA (Brandon et al. 1998; Reiners et al. 2002).
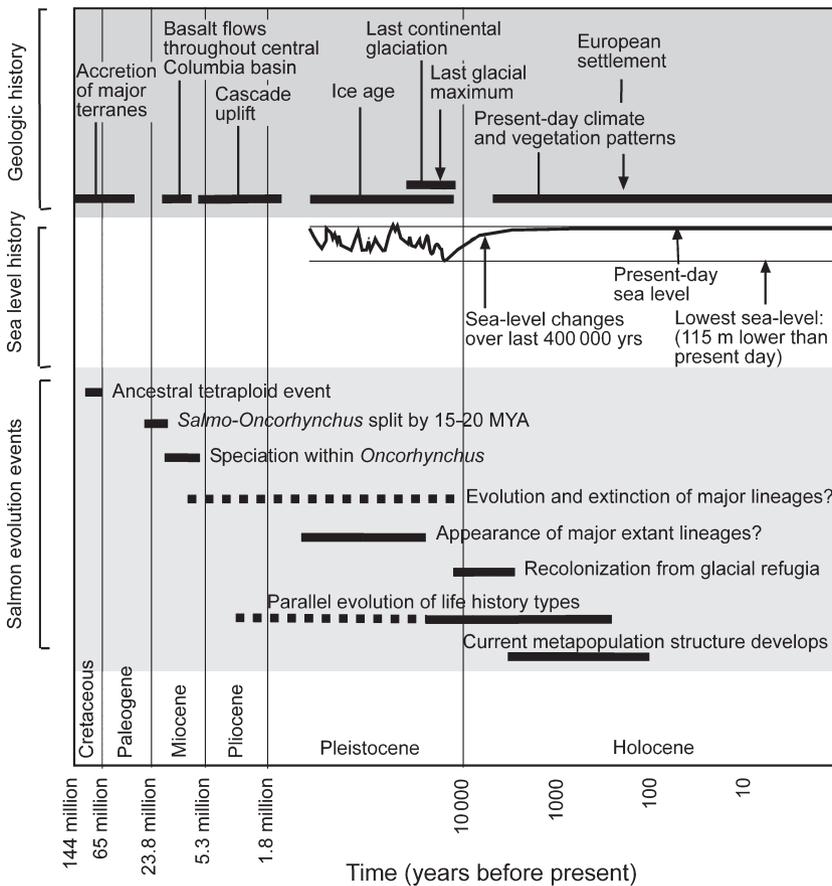

Figure 1 Timeline of major physical and biological events in the evolutionary history of Pacific salmon.

Both the fossil record (Behnke 1992) and molecular data (Devlin 1993) indicate that the genera *Salmo* (Atlantic salmon, brown trout, and relatives) and *Onchorhynchus* (Pacific salmon and western trouts) had diverged by the early Miocene (15–20 MA), perhaps following cooling of the Arctic Ocean (Stearley 1992). By 6 MA, even the most closely related species of Pacific salmon (pink, *Onchorhynchus gorbuscha*; chum, *Onchorhynchus keta*; and sockeye, *Onchorhynchus nerka*) can be distinguished in the fossil record (Smith 1992), indicating that speciation of Pacific salmon occurred in the Miocene. Why are there six species of Pacific salmon (five in North America, plus steelhead) but only one of Atlantic salmon? Montgomery (2000) suggested that Pacific salmon speciation was driven by the active Miocene geologic history of northwestern North America; in contrast, Atlantic drainages have been much more stable over the past 70 million years. Along the Pacific coast, tectonic upliftment created the mountain ranges that characterize the region today, as well as a diverse and dynamic array of habitats that promoted isolation, specialization, and divergence. Unfortunately, Pliocene–Pleistocene fossils of Pacific salmonids are rare (see Smith et al. 2007 for an exception), so we do not know how many other lineages diverged during (and after) the Miocene speciation events but failed to survive.

Forging the major lineages within species: the Pleistocene

Major West Coast river basins had largely adopted their present courses by the Pliocene (Smith et al. 2000) (Fig. 2). However, most of these basins were strongly affected by events during the Pleistocene (0.01–1.8 MA), which was characterized by at least four major ice ages that reworked the surface of the Pacific Northwest landscape. Most of the continental ice sheet was in British Columbia, with three major lobes extending southward into Puget Sound, the Okanogan River basin, and the upper Columbia River basin (maximum extent about 16 000 years before present (ybp) (Richmond et al. 1965; Booth et al. 2003a). The present day geology of the three basins is characterized by deep sedimentary deposits of till, outwash gravels, and lacustrine clays (Booth et al. 2003a). Repeated episodes of glaciation temporarily altered drainage patterns of major river systems, including damming of Puget Sound and forcing river flows southward through the Chehalis valley to the Pacific Ocean (Booth et al. 2003b).

Periodic damming of the Clark Fork River (in present day Montana) impounded much of the upper Columbia drainage in glacial Lake Missoula (Pardee 1910; Smith 2006; Fig. 3). This ice dam breached numerous times over

Figure 2 Some geographic features of the northwestern United States and Canada that are mentioned in the text.
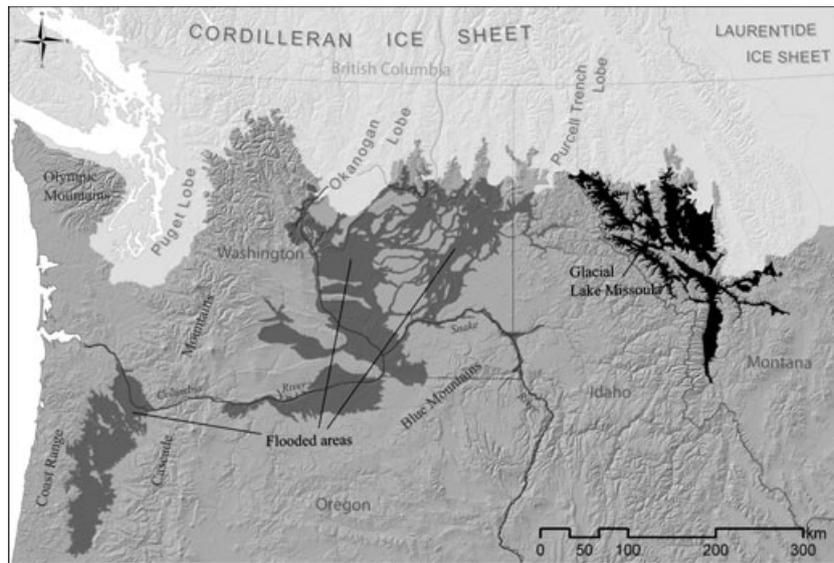
Figure 3 Map of the Pacific Northwest showing areas flooded in the late Pleistocene by periodic breaching of the ice dam that blocked outflow of the Clark Fork River (a tributary to the Columbia River) and created Glacial Lake Missoula.

a period of several hundred years, sending catastrophic 'megafloods' across the Columbia Plateau and down the Columbia gorge to the Pacific Ocean (Waitt 1985; Smith 2006). These floods stripped the land surface to bedrock (creating areas referred to as the channeled scablands; Bretz 1923) and produced enormous fluvial fans and backwater deposits near major ridges and constrictions. The floods affected a large area of the central Pacific Northwest but also left areas of the Cascades, Blue Mountains, and the Snake River basin unaffected by direct scour or deposition by floodwaters (Waitt 1985; Fig. 3). Contemporaneous megafloods (though from earth rather than ice dams) flowed down the Snake River from a paleo-lake near the present day Great Salt Lake in Utah (Malde 1968; Link et al. 1999), and down the Owyhee and Snake Rivers from paleo-lake Alvord/Coyote in south central Oregon (Carter et al. 2006). These floods were considerably smaller and appear to have attenuated significantly before reaching the Columbia River (Malde 1968; Carter et al. 2006).

All of these floods occurred during the last few thousand years of the Pleistocene (*c.* 20 000–12 000 ybp). This period was characterized by alpine glaciers, which covered the highest elevations across Washington, Oregon, and Idaho (Kovanen and Easterbrook 2001; Bishop 2003; Thackray et al. 2004) and excavated large amounts of rock and other material, resulting in wide valleys (Montgomery 2002). These glacial processes continuously delivered large quantities of sand and gravel to moraines, outwash plains, and river systems postglaciation (O'Connor et al. 2003).

These repeated pulses of dramatic environmental and physical habitat changes would have promoted evolutionary changes within Pacific salmon. Ice-free areas along the Bering Sea, the southern Puget Sound/Chehalis basin, the Snake River basin, the lower Columbia River, the Olympic peninsula, and areas to the south served as glacial refugia that provided sources of colonizers during interglacial periods (McPhail and Lindsey 1986). Habitat fragmentation, population bottlenecks, divergence in isolation, and subsequent expansion and hybridization probably all played major roles during this period, but much of this evolutionary history undoubtedly was erased by subsequent glaciations. Some major lineages we see today might date from the Pleistocene – for example, coastal and inland steelhead (anadromous *Oncorhynchus mykiss*), which are considered separate subspecies east and west of the Cascades in the Columbian and Fraser Rivers (Behnke 1992); spring- and fall-run Chinook salmon (*Oncorhynchus tshawytscha* – so named for the season they enter freshwater on their spawning migration) in the interior Columbia and Fraser rivers (Waples et al. 2004); and possibly odd- and even-year pink salmon (Churikov and Gharrett 2002; but see Reisenbichler et al. 2003 for an alternative interpretation). In addition, several other distinct genetic lineages probably originated in the Pleistocene, even though glaciation might not have been directly implicated. These include California Central Valley Chinook and steelhead (Waples et al. 2001); coho salmon (*Oncorhynchus kisutch*) south of Punta Gorda, California (Bartley et al. 1992; Waples et al. 2001); and coastal *O. mykiss* south of San Francisco (Nielsen et al. 1994; Busby et al. 1996).

Forming contemporary patterns of diversity: the Holocene

During the Holocene, two primary modes of landscape dynamics have shaped terrestrial Pacific salmon habitats:

i) long-term processes as sea levels rose and land rebounded after glacial recession and ii) periodic disturbances of varying frequency and magnitude. After glacial recession, characteristics of rivers at and near the glacial margin changed rapidly as they cut down through glacial deposits and developed braided, sediment-laden channels. By 5000 ybp, isostatic rebound and sea level rise in Puget Sound had slowed considerably, shorelines were within a few meters of their present elevations, and climate and vegetation patterns approximated present day conditions (Beechie et al. 2001). Postglacial development of habitats in the interior Columbia basin followed a similar pattern, but the process was delayed in British Columbia because ice retreat occurred several thousand years later. In contrast, coastal rivers south of the ice margin have not been subject to isostatic rebound and dramatic incision, but sea level rise gradually flooded lower basins and shortened rivers.

Superimposed on this gradual progression towards a stable geography are ongoing disturbance regimes ranging from low-frequency, high-magnitude events (megafloods, volcanic eruptions) to high-frequency, low-magnitude events (small landslides, annual floods). Relative frequency and magnitude for these regimes is illustrated in Table 1A. The largest disturbances to salmon habitat during the Late Pleistocene were the Lake Missoula megafloods, which coursed across the Columbia plateau about 100 times during the last glacial maximum, at intervals of approximately 30–70 years (Booth et al. 2003a). These floods probably completely eradicated salmon populations in their path, as rivers would have been reworked every few decades and river channels probably did not develop good quality habitats between floods.

Eruptions from Cascade volcanoes dramatically alter local drainages via landslide deposits and mudflows, but frequency is very low for individual river systems and spatial extents somewhat smaller than for megafloods. After filling with sediment, channels incise for several decades or centuries (O'Connor et al. 2003). Two Cascade volcanoes in particular, Mt. Hood and Mt. St. Helens, have repeatedly erupted in the last 2500 years and sent large quantities of sediment (c. 40–50 million cubic yards) to adjoining rivers (O'Connor 2004).

Temporary barriers caused by large landslides affect salmon throughout the Pacific Northwest, especially when they persist for decades or more and impede migration into major river basins (O'Connor 2004; Table 1A). By contrast, somewhat smaller landslides occur periodically in tributaries but do not cause long-term blockages and are typically circumnavigated by salmonids within days to weeks. Even smaller landslide dams can form and fail during a single flood event, resulting in debris torrents traveling downstream and destroying habitats along the

way. These events have relatively little effect on migration pathways, but can have decades-long effects on habitat quality several kilometers downstream (Johnson 1990).

Present day disturbance regimes are typified by low-magnitude, high-frequency events such as floods and erosion, both of which have relatively small habitat effects compared with the Lake Missoula floods. Floods occur annually throughout the Pacific Northwest, and most extreme events tend to occur during fall and winter storms (Sumioka et al. 1998). Interior rivers typically have more consistent flood magnitudes because of spring snowmelt, but intense summer thunderstorms also create localized flood events. Erosion is driven almost exclusively by high-intensity rainfall events in both forested coastal mountains (where landslides are the dominant sediment delivery mechanism) and interior semi-arid regions (where surface erosion dominates) (Beechie et al. 2003). The vast majority of these erosion events are too small to significantly alter channel morphology, although they can locally reduce salmon survival for one or more years. Under natural storm and fire regimes, frequencies of floods or erosion events vary with basin size (Benda and Dunne 1997a). For example, at the scale of a small tributary (equivalent to an individual spawning reach or deme), a landslide might occur only once in hundreds to thousands of years, and floods large enough to scour redds (salmon nests) might occur once every few decades. As a consequence, tributaries are characterized by infrequent but relatively large disturbances (Benda and Dunne 1997b) and rapid recovery (Beechie 2001), and local demes typically experience large mortality events only once every few salmon generations. At the scale of a salmon population (which generally includes many demes), however, a few demes might typically be affected each year, so the population as a whole experiences a disturbance regime that is less intense but higher in frequency than that experienced at a more local scale. At the larger scale of salmon ESUs (Evolutionarily Significant Units; Waples 1995), disturbance regimes are even more stable, in large part, because the scale of typical storm events is smaller than the ESU. Consequently, an ESU might experience multiple disturbance events each year, but each typically affects only a local area. On rare occasions (tens to hundreds of years recurrence interval), large regional storms can cause extreme floods and erosion events across even large river basins and ESUs (Waananen et al. 1971).

Overlaid on these dynamic processes that shape physical features of salmon habitat are climatic and oceanographic cycles on a variety of temporal scales that profoundly affect salmon productivity (and hence abundance, distribution, and diversity). Even after habitat features stabilized in the Holocene, environmental conditions were not uniformly

Table 1. Characteristics of habitat disturbances in Puget Sound and the Columbia River basin that have affected salmonid evolution and adaptation.

Type	Recurrence interval	Magnitude	Duration	Spatial extent of effect	Location	Time period
A. Natural disturbances						
Continental glaciation	10^4–10^5 years	Several km ice depth	10^4 years in center of ice sheet; 10^2–10^3 years near margins	>10^6 km^2	British Columbia, Puget Sound, Okanogan basin, Upper Columbia River	400 000–12 000 ybp
Alpine glaciation	10^5 years	>100 m ice depth	10^2–10^3 years	c. 10^5 km^2	Cascades, Strawberry Range, Elkhorns, NE Oregon, Klamath Mount	400 000–12 000 ybp
Lake Missoula floods	30 to 70 years	>10^7 m^3/s; >100 m deep	c. 2 weeks/flood; c. 100 floods during c. 2000 years	c. 10^5 km^2	Columbia Plateau and Gorge	13 500–15 700 ybp
Earth dam floods	Single events	10^4–10^6 m^3/s	Days; effects last decades to centuries	<10^3 km^2	U. Snake R. canyon, L. Owyhee and L. Snake	c. 13 000 ybp
Volcanic eruption	100s of years	Multiple valley, aggradation up to 10s of meters	Mudflows can last several days; habitat effects last decades to centuries	Single volcano with multiple watersheds	Cascade range	5 MA–present
Bonneville landslide	Single event	Blocked mainstem Columbia, creating large lake	Days to decades	20 km of river	c. Rkm 65	1670–1760
Contemporary landslides	10s to 100s of years	Centimeters to meters of bed scour and aggradation.	Hours; sediment load present for years to decades	Local stream and downstream area	Cascade range	Ongoing
Floods	Years to decades	Centimeters to meters of bed scour and aggradation	Hours to days	Stream reach to watershed	Entire Pacific Northwest	Ongoing
Drought	10–10^3 years	Extreme low flow conditions	Months	Specific watersheds to regional	Entire Pacific Northwest	Ongoing
Earthquakes	10–10^3 years	Trigger landslides and changes to stream habitat	Minutes (but concomitant landslide effects last years to decades)	Specific watersheds to regional	Entire Pacific Northwest	Ongoing
B. Anthropogenic disturbances						
Anthropogenic barriers	Continual	10–10^3 km of habitat blocked	Years to centuries	Stream to watershed	Entire Pacific Northwest	Ongoing
Channel simplification	Continual	10–10^3 km of habitat simplified	Years to centuries	Stream to watershed	Entire Pacific Northwest	Ongoing
Contemporary landslides	10s to 100s of years	Centimeters to meters of bed aggradation.	Hours; sediment load present for years to decades	Local stream and downstream area	Cascade range	Ongoing
Alteration in flood flows	Years to decades	Peak flow increases of more than 10%	Hours to days	Stream reach to watershed	Entire Pacific Northwest	Ongoing
Alteration in low flows	Years to decades	Moderate reductions to complete loss of summer flow	Days to months	Stream reach to watershed	Entire Pacific Northwest	Ongoing

favorable for salmon. Chatters et al. (1995) identified millennia-scale periods over which freshwater conditions in the Columbia River basin varied dramatically, from 'poor for salmon' (prior to 4000 ybp) to 'optimum for salmon' (c. 2200–3500 ybp) to 'good for salmon' (last 1000 years). In Bristol Bay, Alaska, overall abundance of a multistock complex of sockeye salmon has been remarkably stable over a 50-year period, in spite of major changes in the relative abundance of different contributing stocks, presumably driven by natural changes in freshwater productivity (Hilborn et al. 2003). Just as occurs with habitat disturbances, the climatic effects play out on a variety of spatial and temporal scales. Locally, environmental conditions substantially affect productivity of individual stocks and even stock complexes, but on a broader geographic scale (Bristol Bay) the salmon resource is more resilient because many contributing populations are unaffected at any point in time.

Fluctuations in the marine environment are also an important (albeit poorly understood) component of the evolutionary milieu of Pacific salmon. Finney et al. (2002) used a 2200-year time series of lake sediment cores to estimate millennia scale changes in abundance of Kodiak Island (Alaska) sockeye salmon that they attributed to changes in ocean productivity. Within these century-long trends, they also found evidence for decadal-scale productivity fluctuations of a magnitude comparable to those that have recently been documented to be associated with the Pacific Decadal Oscillation (Mantua and Francis 2004). Fluctuations in productivity can have evolutionary consequences for salmon, mediated through density-dependent processes (Einum et al., in press).

Patterns of diversity in modern salmon populations are the product of three major processes: persistence of some major ancestral lineages (discussed above), recolonization from glacial refugia, and evolution during the Holocene. Major ancestral lineages were preserved in the primary salmon refugia at the last glacial maximum (c. 19 000 ybp). Salmon populations were largely extirpated in the rest of the region (Puget Sound and most of British Columbia were both under ice, and periodic megafloods impacted most of the central Columbia basin), and glacial recession exposed large areas of vacant habitats. Current patterns of diversity in these areas, therefore are largely the product of recolonization and evolution over the last 10 000 years. During the early stages of glacial recession, periodic stream-capture events in low-relief areas allowed mixing of populations from drainages that are typically isolated, such as Puget Sound and the Chehalis River, and the upper Columbia and Fraser Rivers (McPhail and Lindsey 1986). Although salmon have demonstrated an ability to rapidly colonize streams near receding glaciers (Milner 1987), harsh and dynamic postglacial conditions (frigid, unstable, low-productivity streams with high sediment loads) probably would have constrained opportunities for diversification.

By about 5000 ybp, terrestrial salmon ecosystems in the Pacific Northwest had developed most of the characteristics we see today (Beechie et al. 2001). Assuming an average life span of 2–4 years (2 years for pink salmon; 3 years for coho salmon; and 4 years for Chinook, chum, sockeye, and steelhead), the last five millennia have provided about 1250–2500 salmon generations for evolution in relatively stable habitats. Over this period, all but the most isolated populations should have had ample time to reach a dynamic equilibrium between migration, genetic drift, and local adaptation. Pacific salmon diversity is organized hierarchically, with important biological differences identifiable at scales ranging from local populations to more inclusive state and federal conservation units to major lineages within the species (Busack and Shaklee 1995; Kostow 1995; Waples 2006). Contemporary data for molecular markers show a general pattern of isolation-by-distance in most Pacific salmon species – provided distance is measured by stream networks. That is, nearby populations tend to be genetically similar to one another, with larger genetic differences accruing over longer distances (see Waples et al. 2001; Hendry et al. 2004b and references cited therein). Sharper genetic transitions associated with certain geographic features often help to identify boundaries of ESUs (Waples 1995; Waples et al. 2001). These general patterns are consistent with tagging studies, which show that most salmon that stray (do not return to their natal stream to spawn) do so to areas within a few km of the natal stream (Hendry et al. 2004b; Quinn 2005).

Some exceptions occur to these general patterns. Sockeye salmon tends to show a mosaic pattern of genetic structure: nearby populations can be as strongly differentiated as geographically distant ones (Wood 1995; Winans et al. 1996). This pattern reflects the strong association of sockeye salmon with discrete (and often isolated) freshwater lakes. In some species, life history differences are associated with strong genetic distinctions within a geographic area (e.g., odd- and even-year pink salmon in British Columbia and Alaska and spring- and fall-run Chinook salmon in the Interior Columbia River). As noted above, these differences likely reflect divergence that occurred during the Pleistocene.

A recurrent pattern in Pacific salmon is the existence of two or more conspecific life history types within a single geographic area. For example, many river drainages support both spring-run and fall-run Chinook salmon, early- and late-run coho salmon, summer-run and winter-run steelhead, and/or steelhead and resident rainbow trout (Groot and Margolis 1991; Waples et al. 2001).

Joint analyses of genetic and life history data have shown that in most cases, the two life history types within a geographic area are more similar genetically than either is to the same life history type from a different area (see Waples et al. 2004 and references within). This is the pattern predicted to result from repeated, parallel evolution of life history forms, probably in response to spatial variation in environmental conditions (Beechie et al. 2006 and citations therein). Furthermore, molecular genetic differences between the forms within a single geographic area are typically modest and perhaps could be attained following only a century or so of complete isolation (e.g., Waples et al. 2004) – the same time frame over which there is empirical evidence for evolution of Chinook salmon introduced to New Zealand (Quinn et al. 2000, 2001; Kinnison et al. 2008). Given the long period of relative stability of salmon habitats in the Pacific Northwest, it seems more likely that these patterns of diversity reflect a dynamic equilibrium between divergence because of selection and the homogenizing effects of ongoing gene flow. Based on the much higher success rate of stock transfers of freshwater resident than anadromous salmonids (Wood 1995), viability of a Pacific salmon population often depends on execution of a temporal sequence of interactions between its life history and the freshwater and marine environments it inhabits (Allendorf and Waples 1996). The importance of these local adaptations in Pacific salmon has been repeatedly demonstrated since the last major review (Taylor 1991), and this topic is ripe for re-assessment.

The term 'phylogeography' was coined only two decades ago (Avise et al. 1987), but already this approach [which typically focuses on mitochondrial DNA (mtDNA)] has been used to study historical processes responsible for current distributions of a wide range of species. Despite some early interest in phylogeography of Pacific salmon (e.g., Nielsen et al. 1994), most recent genetic analyses have utilized nuclear markers (see Churikov and Gharrett 2002 for a recent exception). Nevertheless, some insights into historical evolutionary processes can be gained by considering the congruence across species in delineation of biological units such as ESUs. Something like this has been attempted recently in a study of evolution of terrestrial ecosystems in the Pacific Northwest (Carstens et al. 2005).

In general, salmon ESUs are groups of populations following largely independent evolutionary trajectories (Waples 1995). The most important factors for defining salmon ESUs are genetic structure at neutral markers (indicative of reproductive isolation) and life history traits and habitat characteristics (both used as proxies for adaptive differences). Based on data summarized by Waples et al. (2001) and references therein, the following

geographic areas are consistently associated with ESU boundaries across multiple salmon species: Central Valley of California (strong contrast with coastal populations), Cape Blanco in southern Oregon (which defines a sharp transition in both marine and terrestrial environments), the mouth of the Columbia River (which separates sharply different environments in coastal Oregon and Washington), the Cascade Mountains (which separate coastal and interior populations in the Columbia and Fraser Rivers), and the Strait of Juan de Fuca (delineating the boundary between Puget Sound and the Olympic Peninsula). These examples show that some geographic/habitat features can strongly shape evolutionary processes across species with a wide range of life histories. Some other geographic features have much less consistent effects. For example, Puget Sound populations of Chinook salmon and steelhead have distinctive genetic and life history features and hence are in separate ESUs from nearby Canadian populations in the Strait of Georgia; in contrast, ESUs of pink, chum, and coho salmon encompass both geographic areas. In Northern California, the southern boundary of the steelhead ESU that starts at Cape Blanco coincides with the southern extent of the Klamath Mountains Geologic Province, whereas the comparable ESU for coho extends to Punta Gorda and that for Chinook as far as San Francisco Bay. In these cases, the evolutionary consequences for salmon are species-specific and reflect specialized interactions of life histories with ecological features of the habitat.

Anthropogenic changes to salmon ecosystems

Native Americans have been important components of Pacific Northwest ecosystems for the past 10 000 years, and during most or all of this period they drew heavily on salmonids as a food source (Butler and O'Connor 2004). Millennia of exploitation probably influenced salmon populations, but it does not appear that this topic has been considered from an evolutionary perspective. In many places throughout the world, human foragers have had substantial effects on exploited populations (Grayson 2001); more locally, Hewes (1973) has argued that catches of Columbia River salmon in the mid-1800s were anomalous and represented a rebound in abundance following decimation of the Native American population by disease, war, and European settlement. If Pacific salmon populations were depressed by Native Americans, one would expect that across the historical record, prime food sources such as salmon would decline in relative abundance compared to lower-ranked prey. However, after analyzing several thousand years of middens in both Puget Sound and the interior Columbia River basin, Butler and Campbell (2004) found a

pattern indicating relative stability rather than change in resource utilization.

A recent analysis (Gustafson et al. 2007) estimated that about 30% of historical salmon populations in the Pacific Northwest and California have been extirpated in the past 200 years, accompanied by losses of comparable portions of major components of ecological, genetic, and life history diversity within the species. Some anthropogenic effects on salmon populations (e.g., harvest, hatcheries) have arguably had large evolutionary impacts, but these topics are covered elsewhere [e.g., Quinn et al. 2007; Hard et al., In press; Araki et al., 2008, Fukuwaka and Morita, 2008, McClure et al., 2008 (b)]. Here, we focus on the consequences of anthropogenic changes to salmon habitats, which have been substantial.

These changes cause loss, degradation, and simplification of salmonid ecosystems, and they also affect the magnitude and/or frequency of disturbance events. Diking and draining of large freshwater marshland habitats (Beechie et al. 2001; Collins and Montgomery 2001), blockage of migration routes (Sheer and Steel 2006), and inundation of river channels by reservoirs (Dauble and Geist 2000) (Table 1B) have all reduced habitat available to salmon. These losses have occurred disproportionately in floodplains and higher-elevation tributary habitat (McClure et al., 2008 (a). Many floodplain habitats have been diked, drained, and isolated from rivers by levees (Collins and Montgomery 2001; Pess et al. 2005b). Some tributaries retain their historical habitat characteristics, but access by salmon is blocked by impassable culverts and other impediments (Beechie et al. 2001). Although each individual habitat loss might have a small effect, collectively they can have important evolutionary consequences by reducing life-history diversity, resilience [Beechie et al. 2006; McClure et al., 2008 (a)], and population size (Beechie et al. 2001). Notably, recent evidence from a study of *O. mykiss* in Idaho has shown that losses of genetic diversity because of cumulative effects of small migration blockages (culverts) were much more substantial than those caused by more dramatic, natural disturbances such as wildfires and landslides (H. Neville, personal communication; October 2007).

Human activities also alter disturbance regimes by increasing landslide rates, disrupting exchange of nutrients and wood in the floodplain, and modifying hydrologic regimes (Ward and Stanford 1995; Collins et al. 2002; Poff et al. 2007). Adaptations of aquatic species can be affected by four attributes of disturbance/flow regimes: magnitude, frequency, duration, and predictability (Lytle and Poff 2004). One of the most pervasive and long-lasting effects on river-floodplain systems is conversion of natural vegetation to agriculture, residential, or industrial

use (Pess et al. 2005b). As impervious surfaces replace native vegetation and soils, delivery of water, sediment, and organic material to the channel is drastically altered (Booth and Jackson 1997). The result is substantial changes to the magnitude and timing of peak flows. In the North Fork Stillaguamish River (Fig. 2) in Puget Sound during the period 1928–49, a flood event of magnitude 750 m^3/s occurred on average only every 10–20 years; during 1972–95, a flood of the same magnitude occurred every year or two (Fig. 4A). Bigger floods have predictable effects on salmonids (more extensive scouring of redds, entombment of eggs by sediment, reduced oxygen in redds because of higher levels of organic matter, and downstream displacement of recently emerged fry),
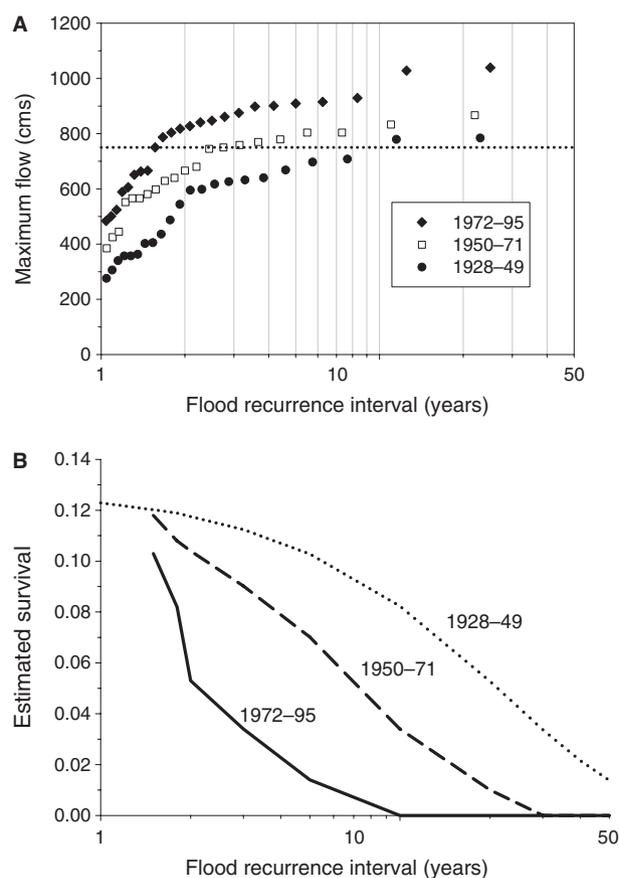

Figure 4 (A) Change over time in the magnitude of flood events in the North Fork Stillaguamish River, Washington, USA. Raw data are largest annual peak flows from a US Geological Survey stream gauge (http://waterdata.usgs.gov/wa/nwis/uv?station=12167000). To calculate the flood recurrence interval, we fit the annual maximum peak discharge data to a log-Pearson Type III distribution using a method of moments approach (US Water Resources Council 1981, Sumioka et al. 1998). (B) Estimates of egg-to-fry survival associated with flood events depicted in the top graph based on the model developed by Seiler et al. (2002) for Chinook salmon from the nearby Skagit River.

leading to generally reduced survival in early life stages (Quinn 2005) (Fig. 4B). Greene et al. (2005) found that as flood recurrence interval decreased, productivity declined in a Puget Sound Chinook salmon population.

Such large changes in the frequency of major flood events can be expected to exert strong directional selection on salmon for changes in behavior (e.g., alter spawn timing to occur earlier or later than large flows) or adult morphology (larger females might be able to deposit eggs below the depth of scour) (Lytle and Poff 2004). However, other factors often constrain the ability to respond through evolutionary change. In fact, the adult size of Puget Sound salmonids has actually declined over the last several decades (Ricker 1981; Weitkamp et al. 1995), because of size-selective fisheries, interactions with hatchery fish, changes in ocean productivity, or a combination of factors. Similarly, changing timing of key life history events can have cascading effects that reduce fitness in subsequent life stages (Waples et al. 2008; Crozier et al. in press), which limits evolutionary flexibility to respond to individual stressors.

Anthropogenic effects on salmon habitats tend to be permanent, at least over ecological time frames, whereas natural disturbances are followed by gradual recovery. For example, dams block migration indefinitely, whereas the vast majority of natural landslides are passable after a few hours or days; even large blockages are eventually worn down. Moreover, human blockages are widespread across the landscape, resulting in large cumulative reductions in habitat availability and diversity, population size (e.g., Beechie et al. 1994; Pess et al. 2005a; Sheer and Steel 2006), and life history diversity (Beechie et al. 2006). The cumulative result – habitat fragmentation – can have particularly severe consequences for species such as salmon that exist in dendritic landscapes, where fragmentation typically results in smaller and more variably-sized fragments, thus reducing metapopulation persistence relative to linear systems (Fagan 2002).

Most land-use changes interrupt process that would recover habitats. For example, a valley-burying volcanic mudflow might cause extensive local habitat change, but river migration and re-establishment of floodplain forests all contribute to natural recovery. In contrast, floodplain habitats isolated by levees and simplified mainstem channels cannot recover by natural processes because rivers are presently disconnected from their floodplains and prevented from migrating (Beechie et al. 2001). Often, habitats altered by humans cannot recover naturally without significant management intervention, which creates a disparity between the temporal scale of disturbance regimes and the conditions under which salmon evolved.

Examples

To illustrate some of these general patterns, we now look in more detail at differences in population genetic structure of Chinook salmon in Puget Sound and the Columbia River and how these differences reflect historical interactions of populations with their dynamic habitats.

Puget Sound

A common index of genetic differentiation is F_{ST}, which measures the fraction of overall diversity that occurs among populations. F_{ST} among Puget Sound Chinook salmon populations is a modest 0.033, several-fold lower than for Columbia River Chinook salmon (Table 2). Nevertheless, some differentiated groups of populations can be identified, the most distinctive being two populations along the Strait of Juan de Fuca at the edge of Puget Sound (Elwha River and Dungeness River, Fig. 5), followed by those in the Nooksack River, at the northern end of Puget Sound.

These patterns can be understood in the context of the processes that shaped Puget Sound habitats in the Quaternary. During the last glacial maximum, much of the water from the Puget Sound lobe drained in a southerly direction through the Chehalis River basin. Although McPhail and Lindsey (1986) hypothesized that the postglacial invasion of salmon into Puget Sound occurred primarily from the ice-free Chehalis River, recent genetic studies indicate a closer genetic affinity of contemporary Puget Sound Chinook with populations from the Olympic peninsula and Vancouver Island (Waples et al. 2004), suggesting a more likely recolonization route through the Strait of Juan de Fuca. The Elwha and Dungeness Rivers were not glaciated, so populations in these streams are

Table 2. Contrasting patterns of population genetic structure in Chinook salmon from Puget Sound and the interior Columbia River.

		Percent		
	Overall F_{ST}	Run/province	Area/run	Sample/area
Puget Sound	0.033	12.3	41.5	46.2
Interior Columbia River*	0.158	79.3	12.9	7.9

*Values shown are unpublished data for an analysis that combines the three provinces described by Waples et al. (2004) from the interior Columbia River.

F_{ST} is a measure of overall genetic differences among populations within each province. The columns on the right show the percent of the F_{ST} that is attributed to differences among run types within provinces among geographic areas within run types, and among samples within areas. Source: Waples et al. (2004) and D. T., unpublished data.
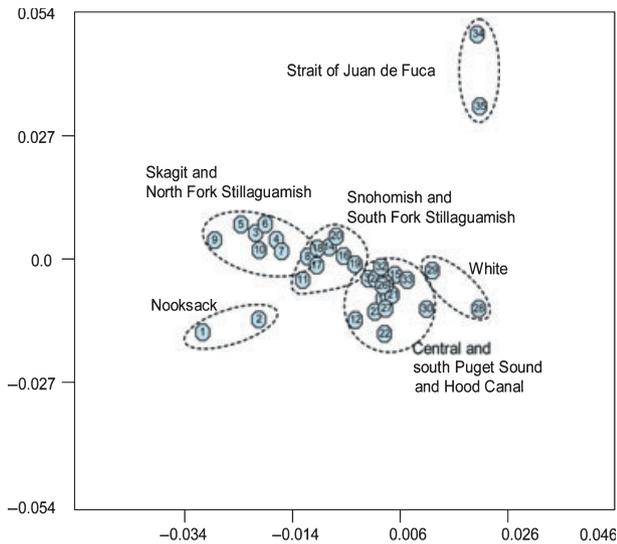
Figure 5 Multidimensional scaling plot of pair-wise genetic distances among populations of Chinook salmon in Puget Sound. Modified from Ruckelshaus et al. 2006.
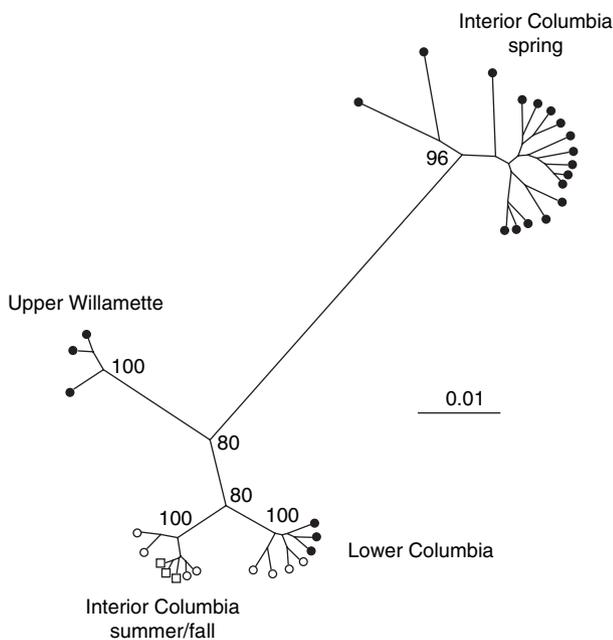

Figure 6 Life history variation mapped onto a tree depicting population genetic structure of Columbia River Chinook salmon. Each population is represented by a symbol indicating the peak run timing (time of entry of adults into fresh water on their spawning migration): solid circle = spring; open square = summer; open circle = fall. Support for the four major genetic lineages (two from the Interior Columbia River, east of the Cascades, and two from west of the Cascades) is indicated by numbers at nodes (percent of 1000 bootstrap replicates having the identical tree topology). Modified from Waples et al. (2004).

probably from older lineages than those from the rest of Puget Sound. Prior to the late Holocene, the Nooksack River flowed north into the Fraser River, and it did not shift to its present course until several thousand years after Puget Sound was recolonized (Pittman et al. 2003).

Although major geologic features in Puget Sound have been relatively stable for the past 5000 years, several factors have limited opportunities for genetic differentiation. First, most of the river basins are too small to allow strong spatial separation and reproductive isolation of different life history types – hence the fraction of population genetic differentiation that can be attributed to adult run timing is small (about 12%; Table 2). Second, periodic localized disturbances (landslides; wildfires; volcanic mudflows from Mount Rainier and Glacier Peak; floods; large-scale tectonic activity along the Seattle Fault Zone) all have occurred over the last few millennia (Booth et al. 2003b). Collectively, these disturbance patterns have determined the temporal and geographic scales on which metapopulation processes play out for Puget Sound salmon. Periodic extirpation of local populations combined with episodic disturbances that lead to widespread straying among drainages tends to retard long-term isolation and divergence.

Columbia River

The Columbia River basin drains an area the size of France and includes salmon habitats in excess of 2000 m elevation and 1500 km from the ocean – providing ample opportunities for strong isolation and population divergence. Moreover, the Pleistocene history of the Columbia River basin was more complex than that of Puget Sound; substantial parts of the Columbia and Snake Rivers were not glaciated, although many of these areas were affected by the late Pleistocene megafloods (Fig. 3).

Evidence that substantial population divergence has occurred can be found in the overall F_{ST} for Columbia River Chinook salmon (0.158; Table 2) – more than twice as large as that found for any other geographic region from California to British Columbia (Waples et al. 2004). Furthermore, genetic differences among populations with different life history traits account for about 80% of the F_{ST} (Table 2; contrast with 12% in Puget Sound). Among Chinook salmon populations from the interior Columbia River (east of the Cascades), all the spring-run populations form one genetically divergent lineage, and all the fall-run populations are from a different lineage. The interior fall-run populations are also genetically similar to both spring- and fall-run populations from the lower Columbia River, west of the Cascades (Fig. 6). Divergence of these two interior lineages almost certainly predates the Holocene and might represent a unique evolutionary event (Waples et al. 2004). Columbia River Chinook salmon also have a rich

diversity of mtDNA haplotypes (Brannon et al. 2004), some of which differ by about 3% in DNA sequence, suggesting that maternal lineages within Chinook salmon are millions of years old – a finding that is consistent with the Miocene speciation event. However, the population lineages appear to be much younger, as common mtDNA haplotypes are found in all major groups shown in Fig. 6.

It is noteworthy that contemporary populations from the interior spring-run lineage are found only in areas of the Columbia basin that had little or no direct effects from the cataclysmic floods associated with Glacial Lake Missoula (Fig. 3). This suggests the possibility that this lineage persisted throughout the Pleistocene in a refuge in the upper tributaries, whereas Chinook salmon reinvaded mainstem areas from coastal refuges in the Holocene. In the lower Columbia River (west of the Cascades), Chinook salmon populations show patterns of genetic structure typical of those from the coast and Puget Sound: at most moderate levels of differentiation among populations within regions, with evidence for repeated, parallel evolution of run-timing diversity (presumably, repeated evolution of the more specialized spring-run populations from the more generalized fall run).

In spite of the size of the Columbia River basin and the wide-spread occurrence of contemporary spring-run populations (well represented in the mid- and upper-Columbia and Snake), overall genetic differentiation within this lineage is relatively low (only slightly larger than for Puget Sound, in spite of occupying a much larger geographic area; Waples et al. 2004 and D. T., unpublished data). That is, although the interior spring-run lineage appears to be of ancient origin, diversification within the lineage is relatively shallow. Ongoing gene flow might explain this shallow divergence, but given the large geographic distances involved a more likely explanation might be that major disturbances to the mainstem Columbia periodically erode emerging genetic differences. For example, the Bonneville Landslide (ca 1450 AD) temporarily blocked the Columbia River and caused a dam 60–90 m high, forming the Cascade Rapids (O'Connor 2004). Oral accounts and archeologic documentation of salmon consumption suggest that the landslide and Cascade Rapids combined with other large features such as Celilo Falls upstream of Bonneville might have resulted in temporary seasonal, yearly, and decadal barriers to fish migration (O'Connor 2004). Something similar happened in the Fraser River in the early 1900s, when the Hells Gate landslide created a severe impediment to migrating salmon (Evenden 2004).

Anthropogenic changes

Recent anthropogenic changes (especially stock transfers and hatchery operations) have perhaps blurred population structure in Chinook salmon but have not obscured the major historical patterns described above. In both Puget Sound and the Columbia River, however, disproportionate losses of upper level tributary habitat and wetland and estuarine habitats have reduced diversity of life history trajectories that can be supported [Bottom et al. 2005; McClure et al., 2008 (a)]. Urbanization and other land-use patterns have dramatically changed flow regimes, creating new selective pressures. A series of major hydroelectric dams in the Columbia River basin extract a demographic 'tax' on anadromous populations (e.g., Kareiva et al. 2000), but until recently the evolutionary consequences of these structures had attracted little attention. Waples et al. (2008) identified a number of dam-related changes to selective regimes that should cause an evolutionary response in salmon, including: i) transformation of the free-flowing Columbia River into a series of slack-water reservoirs that dramatically alter both juvenile and adult migration; ii) flow patterns now deliver some juvenile salmon to the Columbia River estuary later than is optimal for ocean survival, but counteravailing selective pressures might constrain evolution toward earlier migration; iii) reservoirs are a benign environment for non-native species that compete with and prey upon salmon. [Some of these points are also emphasized by Crozier et al. (in press)]. Similar (albeit usually smaller) dams occur on many rivers in Puget Sound and other regions within the range of Pacific salmon.

Synthesis and discussion

During their long evolutionary history, Pacific salmon have had to deal with formidable environmental changes on a wide variety of spatial and temporal scales. Miocene diversification of *Oncorhynchus* provided an opportunity for at least six million years of evolution within each species, but no extant, intraspecific lineages are anywhere near that old. The dramatic Pleistocene climactic oscillations probably exterminated many lineages for which we have no empirical evidence. Contemporary patterns of diversity reflect a combination of persistence of some major ancestral lineages that presumably diverged during the Pleistocene, recolonization (and subsequent mixing) from glacial refugia, and *in situ* evolution during the Holocene.

Following approximately 5000 years of relative habitat stability, metapopulation structure of most Pacific salmon should have reached a quasi-equilibrium with respect to migration, genetic drift, and natural selection. Within that time span, periodic disturbances and geographic constraints have interacted with salmon life history to limit the strength of divergence we see in contemporary populations. Events that occur only rarely on any given local scale are common on the larger landscape, creating a

dynamic and shifting mosaic of younger and older lineages. Occasional events that affect large geographic areas, as well as periodic bottlenecks associated with cycles of poor marine and/or freshwater productivity, can erode existing diversity that has built up over decades, centuries, or millennia, thus resetting the evolutionary clock.

Although we have focused on historical processes and populations in two geographic areas, many of the general patterns should be applicable to other areas affected by continental glaciation. Even many unglaciated areas such as coastal Oregon and California would have been affected by sea-level fluctuations, alpine glaciations, and climate fluctuations. A recent analysis of historical habitat disturbance regimes along the Oregon coast, and how these have been (and will be in the future) affected by anthropogenic changes (Burnett et al. 2007), parallels many of the themes identified above.

We expect that responses to future evolutionary challenges will vary by species. Pink and coho salmon have the most canalized life histories and hence the least flexibility, with fixed (pink) or nearly fixed (coho) ages at smolting and spawning (Waples et al. 2001). These species use temporal replication of quasi-separate lineages to ensure persistence, but they can be vulnerable to changes in temporal scales of disturbance regimes. Notably, coho salmon have disappeared from almost half of the major ecological provinces they once occupied in northwestern North America (Gustafson et al. 2007). Chinook salmon and steelhead exhibit the most diverse array of life history strategies, both within and between populations (Groot and Margolis 1991; Waples et al. 2001; Quinn 2005), and they remain well distributed in historical habitats (Gustafson et al. 2007) – and in the case of *O. mykiss*, via resident forms in areas above impassable migration barriers. However, as noted above, even these species have experienced disproportionate losses of stream-maturing populations associated with specific habitat types, and anthropogenic disturbances (such as dams) that increase the cost of migration can selectively favor nonmigratory forms of *O. mykiss* and *O. nerka* (Hendry et al. 2004a; Waples et al. 2008; see also Thériault et al., in press).

The failure of most stock transfers suggests that many, perhaps most, Pacific salmon populations are not ecologically exchangeable *sensu* Crandall et al. (2000). It seems reasonable to assume that at any given point in the past, a similar pattern of locally adapted populations would have occurred across the range of Pacific salmon. If we could compare these patterns of adaptation across time, what would they look like? A few lineages (e.g., interior Columbia River spring-run Chinook salmon, which express a tightly-correlated suite of juvenile and adult life history traits) appear to be relatively ancient and to have survived the Pleistocene disruptions (however, all remaining US populations from this lineage are currently listed as threatened or endangered species under the US Endangered Species Act). In many other cases, local populations occupy habitats that have experienced substantial fluctuations in quality over decades, centuries, and millennia. Thus, we might expect that if we could take a snapshot of Pacific salmon populations at several times in the past, we would consistently find (as we do now) a mosaic pattern of local adaptation, but that the fine-scale details of the pattern might differ across time periods.

How fast can Pacific salmon evolve? Quite rapidly on geologic time scales, as evidenced by the rich store of intraspecific diversity found in deglaciated areas such as Puget Sound and British Columbia. But evidence is also accumulating that documents evolution within human life times, particularly associated with introductions into novel habitats. In a century since being introduced to New Zealand, Chinook salmon have developed genetically based differences in life history traits (Quinn et al. 2000, 2001) that are comparable to those found between different populations within Puget Sound or other ESUs of Pacific salmon. But these measures based on mean trait values might underestimate the strength of local adaptation. Kinnison et al. (2008) found that fitness differences (measured by vital rates) between diverged populations of New Zealand Chinook salmon are several-fold larger than mean differences in life history traits.

Recent anthropogenic changes to salmon habitats present new evolutionary challenges for the species. Although none of the changes (to date) rivals the Pleistocene glaciations in severity or duration, several novel features are noteworthy. Some anthropogenic changes are small in magnitude but replicated many times across the landscape (e.g., culverts), leading to pervasive effects on population structure and fragmentation. Other changes alter the relationship between magnitude and frequency (Fig. 4) or geographic scale of disturbance regimes, potentially upsetting carefully tuned adaptations. When high mortality is associated with disturbances, coarse-grained disturbances have a particularly strong influence on life history evolution (Lytle 2001). Many human alterations of salmon ecosystems can be expected to persist indefinitely, thus precluding natural recovery. Finally, if habitats continue to be degraded but recruitment of new, high quality habitat is precluded, Pacific salmon will experience a downward spiral of usable habitat.

Responses by Pacific salmon populations to these challenges can be of four general types:
1. adapt to new selective regimes (evolutionary change);
2. tolerate the new conditions without genetic change (phenotypic plasticity);

3. change their distribution in concert with environmental changes;

4. go extinct.

Each of these responses might be important in particular circumstances, but at present we lack the ability to reliably predict which is most likely for a given situation. If salmon populations do not move or go extinct, they must either evolve or deal with environmental changes through phenotypic plasticity. Although phenotypic plasticity is well documented in Pacific salmon (e.g., Beckman and Dickhoff 1998), its limits are not. Similarly, Pacific salmon have been shown to have a heritable component to expression of many life history traits (reviewed by Carlson and Seamons, in press). However, we lack a general understanding of how rapidly and under what conditions, evolutionary change can be expected to occur in salmon. Can phenotypic plasticity, substantially buffer Pacific salmon against climate and other anthropogenic changes (Crozier et al., in press)? Can these species evolve fast enough in response to changes they cannot accommodate through plasticity – that is, can evolution make the difference between population extinction and persistence (Kinnison and Hairston 2007)? What happens if a population evolves a life history that is adapted to anthropogenically altered conditions, and subsequently the habitats are restored to something resembling their pristine state (see Williams et al., in press)?

The analysis by Gustafson et al. (2007) makes it clear that although many populations of Pacific salmon have been extirpated and major components of historical diversity have been lost, much (in most cases the majority) still remains. With the human footprint on natural ecosystems rapidly increasing, Pacific salmon appear to be at a critical juncture in their evolutionary history. If the bulk of current diversity can be conserved, the species should be robust and resilient enough to continue to be major players on the evolutionary stage. However, half the remaining populations in the contiguous US are considered threatened or endangered, and if they were lost the fabric of diversity might be so tattered that long-term persistence would be in doubt. A key factor in determining which of these outcomes is more likely will be whether anthropogenic changes can be shaped to produce disturbance regimes that more closely mimic (in both space and time) those under which the species have evolved. If this can be accomplished – that is, if humans can provide conditions that allow essential evolutionary processes to continue (Moritz 2002) – Pacific salmon should be well equipped to deal with future challenges, just as they have throughout their evolutionary history.

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