significant differences between samples from the upper Fraser River and the lower coastal mainland of British Columbia. However, because some rare alleles were shared between the latter two areas, Wehrharn and Powell concluded that there are no absolute barriers to dispersal of coho salmon between the lower coastal mainland, lower Vancouver Island, and the Fraser River.

Ecological/Genetic Diversity

Several types of physical and biological evidence were considered in evaluating the contribution of coho salmon from southern British Columbia, Washington, Oregon, and California to the ecological/genetic diversity of the biological species throughout its range. Factors examined included: (1) The physical environment—geology, soil type, air temperature, precipitation, river flow patterns, water temperature, and ocean conditions/upwelling; (2) biogeography—marine, estuarine, and freshwater fish distributions, and vegetation; and (3) life-history traits—smolt size and outmigration timing, age and size at spawning, river entry timing, spawning timing, and marine coded-wire-tag (CWT) recoveries. The relative magnitudes of potential human-induced genetic changes were also considered. The physical and zoogeographic evidence supporting the delineation of each ESU is addressed under ''ESU Determinations.'' Because life history traits provide important insight into the ecological/genetic diversity of the species and can reflect unusual or distinctive adaptations that promote evolutionary processes, a more detailed discussion has been provided below.

Coho salmon life-history traits that show some regional variation include river entry and spawning timing, age at maturity, and marine CWT recovery patterns. River entry and spawning timing patterns of coho salmon are considerably variable in time and space, but some regional patterns exist. Puget Sound coho salmon typically enter the rivers in October, but some basins have very early and late runs. Along the Washington coast, river entry generally occurs in October, with a few exceptionally late or early runs. Historically, Columbia River coho salmon entered fresh water from August through December, while Oregon coho salmon enter rivers in October. Coho salmon in southern Oregon and northern California also enter rivers in September or October. River entry is much later south of the Klamath River Basin, occurring in November and December in basins south of the Klamath River to the Mattole River, CA, and from mid-December to mid-February in rivers farther south.

Spawning timing shows less variation than river entry, but it has similar patterns. Along most of the Washington and Oregon coasts and in Puget Sound, coho salmon spawn in November and December, with exceptionally early and late runs occurring along the Washington coast, in the Columbia River, and in Puget Sound. Spawning in southern Oregon and northern California also occurs in December, but south of the Mattole River it occurs most frequently in January. Because coho salmon enter rivers late and spawn late south of the Mattole River, they spend much less time in the river prior to spawning than do coho salmon farther north. Coho salmon adults in the three-state area overwhelmingly (>95%) spawn at age 3, spending just over a year in fresh water and a year and a half in the ocean (Sandercock 1991). In contrast, many coho salmon adults from southeast Alaska spend over 2 years in fresh water and return to spawn at age 4. It is not known exactly where the transition occurs between these two age structures, but limited information suggests that an increasing proportion of 2 year-old smolts is seen in coho salmon as one approaches the north end of Vancouver Island from the south.

The life-history trait showing the clearest differentiation coastwide is the pattern of ocean distribution inferred from marine recoveries of hatchery fish carrying CWTs. These data, from the Pacific States Marine Fisheries Commission's regional Mark Information System, show that marked coho salmon from southern Oregon and northern California are most frequently recovered from California coastal waters (65 to 92 percent), with some recoveries off Oregon (7 to 34 percent), but almost none off Washington or British Columbia. In contrast, coho salmon from the Oregon coast north of Cape Blanco are recovered primarily in Oregon waters (57 to 60 percent), with significant appearance in California (27 to 39 percent), and low but fairly consistent recovery levels from British Columbia (2 to 6 percent) and Washington (2 to 9 percent). Compared to the Oregon coast populations, Columbia River populations have approximately the same proportion of British Columbia (2 to 16 percent) and Oregon (36 to 67 percent) recoveries, but the California recoveries are considerably lower (1 to 15 percent) and the Washington recoveries correspondingly higher (22 to 54 percent).

Populations from the Washington coast, Puget Sound, and British Columbia have much more northern recovery patterns than those from either the Columbia River or the Oregon coast, although distinctive patterns within Washington and British Columbia are not as obvious as those for groups farther south. Coho salmon released from central British Columbia were frequently recovered off Alaska (15 to 39 percent), with the remainder of the recoveries coming from British Columbia (61 to 85 percent). Coho salmon released along the east and west coasts of Vancouver Island and the southwest British Columbia mainland are caught almost exclusively in British Columbia (90 to 99 percent), with infrequent recoveries in Alaska (less than 1 percent), Washington (0 to 9 percent), and Oregon (less than 2 percent). Coho salmon released from Puget Sound, Hood Canal, and the Strait of Juan de Fuca are recovered from Washington (23 to 72 percent), British Columbia (27 to 74 percent), and Oregon (0 to 3 percent), with essentially no recoveries from Alaska or California. Coho salmon from the Washington coast have similar CWT recovery patterns, but have higher Oregon recoveries than Puget Sound/Hood Canal coho salmon.

Because Puget Sound and Hood Canal coho salmon are caught at high levels in Puget Sound, an area not entered by coho salmon from other areas, recoveries from this area might be considered an extension of freshwater recoveries, which were excluded from the above analyses. Removing Puget Sound recoveries from total Washington marine recoveries results in Puget Sound and Hood Canal coho salmon recovery patterns that are intermediate to those of British Columbia and the Washington coast.

Genetic Changes Due to Human Activities

The effects of artificial propagation and other human activities can be relevant to ESA listing determinations in two ways. First, such activities can genetically change natural populations so much that they no longer represent an evolutionarily significant component of the biological species (Waples 1991). For example, in 1991, NMFS concluded that, as a result of massive and prolonged effects of artificial propagation, harvest, and habitat degradation, the agency could not identify natural populations of coho salmon in the lower Columbia River that qualified for ESA consideration. Second, risks to the viability and genetic integrity of native salmon populations posed by human activities may contribute to their threatened or endangered status (Goodman 1990, Hard