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Salmon at River's End:

The Role of the Estuary in the Decline and Recovery of Columbia River Salmon

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The Role of the Estuary in the Decline and Recovery of Columbia River Salmon

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Executive Summary

The continued decline of Columbia River salmon (*Oncorhynchus* spp.) populations has long focused concerns on habitat changes upriver, particularly the effects of large hydroelectric dams. Increasing evidence that ocean conditions strongly influence salmon production, however, has raised questions about the importance of the estuarine environment to salmon and whether the hydropower system has affected estuarine-rearing habitats. In response to Northwest Power Planning Council recommendations, we initiated a review of what is known about the effects of the hydroelectric system on the hydrology, habitats, and ecology of the Columbia River estuary. Our goal was to develop recommendations for improving estuarine conditions or to identify research that may be needed before appropriate salmon-management changes can be defined. Our review and analyses addressed four major questions:

1) What habitats and processes support native salmon populations during the estuarine phase of their life cycle?
2) Have changes to the estuary had a significant role in salmon decline?
3) What have been the impacts of flow regulation on the hydrology, habitat, and biological interactions in the estuarine ecosystem?
4) What estuarine conditions are necessary to maintain salmonid diversity in the Columbia River basin?

Conclusions and Recommendations

The results indicate that habitat and food-web changes within the estuary and other factors affecting salmon population structure and life histories have altered the estuary's capacity to support juvenile salmon. Diking and filling activities that decrease the tidal prism and eliminate emergent and forested wetlands and floodplain habitats have likely reduced the estuary's salmon-rearing capacity.

However, simplification of the population structure and life-history diversity of salmon possibly is the most important factor affecting juvenile salmon performance. In the absence of data on present-day estuarine use by wild, subyearling ("ocean-type") salmon, we concluded that basin-wide upriver habitat losses, overharvest, and production-oriented hatchery management practices clearly influence patterns of salmon abundance, diversity, and residency in the estuary.

Restoration of estuarine habitats, particularly diked emergent and forested wetlands, and flow manipulations to restore historical flow patterns might significantly enhance the estuary's productive capacity for salmon. It is possible that historical changes in population structure and salmon life histories, however, prevent salmon from fully utilizing the productive capacity of estuarine habitats even in their presently altered state. Therefore, efforts to improve or restore the estuary for salmon must be developed in concert with hatchery, harvest, and upriver habitat improvements to recover those life history types that can benefit from estuary restoration.

A sound historical and evolutionary context for interpreting modern estuarine habitat conditions and for developing salmon recovery strategies is needed. Without proper context, recovery actions may inappropriately target those few salmon life history types and habitats that are abundant today, further reinforcing salmon decline symptoms rather than expanding the basin's productive capacity. A strategy that continues emphasis on improving survival of a few Chinook salmon (*O. tshawytscha)* dominant types, particularly large hatchery yearlings and subyearlings with short estuarine residence times, may further narrow the distributions of size, migration timing, and rates of migration. This would result in concentrated use of the estuary and thus would prevent salmon from utilizing its full productive potential.

While the extinction risk of many Columbia River populations implies the need for immediate recovery action, lack of data on estuarine habitat use by salmon requires that further study may be necessary before we can define appropriate restorative measures. Both of these concerns can be addressed by simultaneously initiating targeted restoration activities, where there is reasonable confidence in their ecological benefits, and collecting new data to better understand salmon habitat requirements and restoration needs. To achieve these ends, the following specific recommendations are offered:

Adopt an Explicit Ecologically Based Conceptual Framework for Estuary Management and Restoration

The lack of an explicit ecological framework for salmon conservation is a fundamental impediment to recovery efforts in the Columbia River basin. Such a framework is particularly important to direct recovery efforts in the estuary, where physical and biological interactions are complex and continually changing in response to tidal forces, river flows, and seasonal fluctuations in the composition of species assemblages.

The lack of information about the estuarine-rearing requirements of juvenile salmon is the result of a long-standing "production" approach to salmon management and research. This approach assumes the estuary is a simple migration corridor in which mortality factors must be controlled, rather than a productive nursery ground where the varied habitat needs of diverse populations and life history types must be protected.

In the estuary, the ecological requirements of salmon also must be placed in the broader context of factors at other life stages that shape population structure and life history. These factors determine whether juvenile salmon can realize the full productive potential of the estuary. We adapted a conceptual framework for this assessment (i.e., the "member/vagrant" hypothesis) that accounts for life cycle linkages to salmon performance in the estuary and for the diverse life histories and resilience of Columbia River populations.

Protect and Restore Opportunity for Salmon to Access Emergent and Forested Wetlands in the Estuary and Riparian Wetlands in the Tidal Floodplain

Historical losses of peripheral floodplain, wetland, and riparian habitats from diking and filling activities in the Columbia River estuary have reduced available rearing habitat for salmon with subyearling life histories. Such effects may not be limiting to yearling, stream-type juveniles at present because hatcheries, harvest, and upriver habitat losses tend to favor these life histories. Any effort to increase life history diversity, however, will require reestablishment of important rearing habitats that have been substantially modified or removed from the estuary.

Studies in other Northwest estuaries indicate that wetland restoration could offer a cost-effective method to improve salmonid rearing conditions. Reestablishment of more natural flow regimes in the basin might also diversify estuarine habitat opportunity and its associated variety of salmon rearing and migration behaviors.

Reacquire Phenotypic Diversity of Salmon, Including a Broader Range of Sizes, Times of Entry, and Periods of Residency in the Estuary

Although increased genetic and life history diversity of salmon may ultimately require long-term expansion of habitat opportunity upriver and in the estuary, rapid progress in the use of existing or restored habitats could be made by expanding phenotypic diversity of salmon now heavily influenced by hatchery programs. Such improvements could require reductions in hatchery releases or changes in hatchery rearing practices.

Any management changes to benefit salmonid use of the estuary, however, will require an improved accounting system and a greater degree of coordination of basin-wide hatchery programs than presently exists. For example, incomplete records of hatchery release groups, variations in rearing and release practices that confound interpretation of management effects, and difficulties in distinguishing the hatchery or wild origin of unmarked salmon preclude a full accounting of the influence of hatchery practices on salmon behavior and performance in the estuary.

Monitor Variations in Life History Diversity, Habitat Use, and Performance of Juvenile Salmon in the Estuary

Because the abundance and life histories of salmon in the estuary are linked to source populations and habitats upstream, changes in life history diversity and the relative proportions of wild juveniles in the estuary may indicate whether recovery efforts are working basin wide. Unfortunately there is no established monitoring program to describe long-term trends in salmon rearing behaviors in the estuary. Since 1914–1916, neither salmon scales nor otoliths have been collected or archived to evaluate changes in estuarine life history patterns.

Most contemporary estuarine studies are of short duration, including numerous local-impact studies, and only rarely have they sampled many of the shallow habitats typically preferred by smaller subyearling salmon. Furthermore, the most consistent monitoring in the estuary has emphasized the migration rates and survival of large, hatchery-tagged fish, and poorly represents wild, ocean-type species and life histories that are likely most dependent upon estuarine conditions. A more representative sampling program is needed to monitor variability in the estuarine life histories and performance of salmon.

Review the Scientific Basis for Proposed Habitat and Bathymetric Changes in the Estuary Relative to the Restoration Goals of the Columbia Basin Fish and Wildlife Program

Habitat changes and economic activities within the estuary have been evaluated independently of management or restoration efforts that affect salmon and their habitats elsewhere in the Columbia River basin. For example, the potential effects of ongoing or proposed estuarine dredging, spoil disposal, or habitat-restoration activities on the Columbia Basin Fish and Wildlife Program have not been explicitly evaluated.

Because all anadromous salmonids in the Columbia River pass through or rear in the estuary before migrating to the ocean, changes in estuarine conditions could determine the effectiveness of salmonid recovery efforts throughout the basin. Modeling results show that estuarine habitat opportunity for salmonids is sensitive to bathymetric change. In addition, the response of predacious birds to artificially created dredge-spoil islands in the lower estuary illustrates that at least some estuarine habitat changes may have unexpected ecological consequences.

Impact assessments associated with dredging and disposal activities usually have focused on localized impacts and have not considered salmonid responses to changes in habitat opportunity or capacity at a landscape scale. Nor have the assessments considered the history of incremental change upon which each new project is superimposed or the broader responses of the ecosystem to physical habitat modifications.

Use Physical Observations and Hydrodynamic Modeling to Assess the Effects of Bathymetric Change, Flow Regulation, and Alternative Restoration Designs on Habitat Opportunity for Juvenile Salmon

The hydrodynamic model applied in this assessment has proven to be a useful approach for evaluating the relative effects of flow modification and bathymetric change on habitat opportunity for salmon. However, its present application is limited by several critical data gaps, including the lack of present-day, high resolution bathymetric data and physical observations for shallow regions of the estuary. For example, the ability of the model to characterize physical habitat opportunity relative to the depth criterion (much more so than opportunity determined with respect to the velocity criterion) was very sensitive to assumed bathymetric configurations in the shallow areas of the estuary. This emphasizes the need to obtain accurate bank-to-bank bathymetric data for the lower river and estuary for improved understanding of the river flow impacts on physical habitat opportunity.

Review Results of Estuarine Predation Studies in the Context of Salmon Population and Habitat Change

It is unclear whether the high rates of salmon predation by Caspian terns (*Sterna caspia*) and other marine birds in the estuary is a significant factor affecting salmon recovery or an ecological symptom of other changes. Those changes might include alteration of estuarine habitats, simplification of the geographic structure of salmon populations, and reduced variation in salmon rearing and migration behaviors.

High juvenile salmonid predation rates, however, could result from replacing a broad continuum of salmon life history types with punctuated releases of large hatchery fish that are concentrated in relatively few estuarine habitats over reduced time periods. Hatchery-induced changes in surface-feeding behavior also could be a factor increasing the vulnerability of salmon smolts to predators. Emphasis on estimating predation rates alone thus may lead to inappropriate salmon recovery proposals unless these results are evaluated in a broader historical and ecological framework.

Assess the Effects of Altered Habitats and Food Webs on the Capacity of the Estuary to Support Juvenile Salmon

The results indicate that a variety of ecological changes may have affected the estuary's capacity to support wild subyearling Chinook salmon. These changes include loss of floodplain and other wetland habitats, the effects of climatic changes on physical processes and estuarine food webs, interactions with an increasing number of nonindigenous species, and shifts in the timing of established patterns of river flow and salmon migrations. The direction or magnitude of these ecological changes, unfortunately, cannot be assessed from the limited empirical data available.

The effects of altering food-web sources through habitat modifications, for example, have not been directly evaluated. We also have little data to assess the effects of a two-week advance in the spring freshet because of flow regulation and a substantial delay in peak salmon migrations because of hatchery and other influences. If estuarine prey-production cycles and salmon-migration behaviors are adaptive and linked to flow variations, then such changes could create a mismatch between salmon and their prey resources, reducing the productive capacity of the estuary.

Changes in the coarse and fine sediment budgets, particularly the quality of organic matter input to the system, also are poorly understood.

Research Approach and Results

The first two sections establish the context for this evaluation, including a review of historical changes throughout the basin that have affected salmon and estuarine habitats, and the conceptual framework upon which our analyses and interpretations are based. The subsequent four sections describe results of the following analyses:

- A review of climatic variations and human-induced changes in river flow during the past 140 years that have influenced estuarine-rearing opportunities and capacities for Columbia River salmon.
- An evaluation of simulation modeling to understand the dynamics of salmon habitat opportunity within the estuary.
- An assessment of ecological changes in the estuary that could affect the capacity of estuarine habitats to support salmon.
- An analysis of historic changes in the estuarine performance of salmon using indicators of growth and life history variation.

From the results of these analyses, we reexamine the validity of our conceptual framework and its implications for salmon and estuarine-habitat conservation.

The principal findings of each of these chapters are briefly summarized below:

Estuarine Development History and Salmon Decline

Industrial development of the Columbia River and its estuary and declines in salmon populations are well documented. The effects of intensive harvest were apparent throughout the Columbia River basin by 1911, just as dam construction and irrigation diversion were beginning, and alterations to the estuary for navigation were unfolding. Increased salmon-conservation measures and management initiatives, however, coincided with the decline in freshwater habitat, regulation and diversion of river flow, and estuarine habitat loss and degradation.

Installation of hydroelectric and irrigation diversion dams without providing for fish passage reduced salmon spawning and rearing habitat by 55%. Today, 23 mainstem and more than 300 tributary dams regulate the flow of the Columbia to the Pacific Ocean. Through this development history, the Columbia River became progressively channelized and detached from its floodplain.

Approximately 65% of the tidal marsh and swamp habitat below Jones Beach (RKm 75) in Oregon had been diked or filled by the middle of the 20th century. The loss of these habitats between Jones Beach and Bonneville Dam (RKm 235) was likely greater but has not been quantified. Many other activities have degraded habitat throughout the estuary including upland logging and agriculture, shoreline armoring, construction of over-water structures, removal of large wood, and channel deepening and widening.

In order to compensate for habitat losses and salmon decline, resource managers developed intensive hatchery programs that substituted concentrated releases of a few artificially produced stocks for the more diverse populations and life-history types that were formerly distributed throughout the watershed. As a consequence of these and other factors addressed in this analysis, historical Columbia River salmon returns between 11 million and 16 million fish annually have now declined to fewer than 12% of predevelopment levels.

A Conceptual Framework for Evaluating Estuarine Habitat Conditions

An agricultural approach to fisheries management that sought to eliminate apparent production “bottlenecks” has long ignored the estuary’s role in supporting salmon populations. A fundamental impediment to salmon and estuary recovery, therefore, is the lack of a conceptual framework that adequately explains the evolutionary and ecological requirements of diverse salmon populations.

For this assessment, we adapted a conceptual framework (the “member/vagrant” hypothesis) that was developed to explain the dynamics and population richness of marine species with complex life cycles. The member/vagrant hypothesis suggests that life history diversity in salmon is based on the geography of local, self-perpetuating populations and the variety of habitats that can support salmon life cycles. A crucial assumption of this framework is that the resilience of Columbia River salmon to natural environmental variability is embodied in population and life history diversity, which maximizes the ability of populations to exploit available estuarine rearing habitats. This framework recognizes variation in rearing behavior (phenotypic diversity) as the result of diverse salmon genotypes interacting with unique habitat features, including those within estuaries.

These interactions result in a variety of alternative behavioral "solutions" for salmon to successfully complete their life cycles, such as variations in the timing and age of migration, duration of residency in the river and estuary, and size at ocean entry. The total productive capacity of the Columbia River basin for salmon, therefore, is a function of all combinations of genotype and habitat that allow for the full expression of salmon rearing and migration behaviors, including diverse life histories in the estuary.

Any changes that sever the link between salmon behavior and habitat may affect the productive potential of the Columbia River estuary, for example:

- removing or degrading estuarine habitats that salmon require to express the full diversity of potential rearing behaviors,
- altering the geographic structure or genetic characteristics of component populations throughout the basin that converge in the estuary en route to the ocean, or
- directly altering the phenotypic behavior of salmon through hatchery rearing and release practices, transportation of fish around dams, etc., regardless if the underlying genetic structure of populations is affected.

In this evaluation, an effort was made to distinguish the role of the Columbia River hydropower system from other factors that influence the salmon rearing capacity of the estuary, including phenotypic or genetic effects that can determine whether salmon fully utilize this capacity. Our analyses emphasized subyearling "ocean-type" Chinook salmon, because this life history type makes maximum use of estuarine habitats and likely would be most sensitive to changes affecting the estuary. However, results of these analyses also should apply to other salmon species with "ocean-type" life histories, particularly chum salmon.

Changes in Hydrological Conditions

The magnitude and timing of river flow, which significantly influence estuarine habitat of juvenile salmon, have been highly modified at the watershed level. The predevelopment flow cycle of the Columbia River has been totally reshaped by hydropower regulation and irrigation withdrawal. While there is a prominent climate signal in river-flow variability over the period of the analysis (1859–present), the magnitude of maximum spring-freshet flow has decreased more than 40% from the predevelopment period (1859–1899) to the present. Flow regulation is responsible for approximately 75% of this loss, irrigation withdrawal for approximately 20%, and climate change for approximately 5%.

The timing of maximum spring-freshet flow also has changed, primarily because of hydropower and irrigation development upriver, resulting in an approximate two-week shift earlier in the year (mean predevelopment date of 12 June compared to modern mean date of 29 May). Flow regulation now exacerbates early maximum spring-freshet peak flows, such as the 23 April freshet peak in the year 2000. Gradual climate warming also has contributed to the change in freshet timing. Also, the annual average flow at the mouth has been reduced from about 8,500 m^3s^{-1} to less than 7,000 m^3s^{-1}, with climate change and water withdrawal each responsible for approximately 50% of the reduction.

Changes in hydrology have had a significant impact on salmon habitat. Suppression of winter- and spring-freshet flows, compounded by flood-control diking and wetland reclamation below Bonneville Dam, has greatly reduced the frequency of overbank flows. Thus salmon rearing habitat in riparian areas and backwater channels has been blocked during flood events, and the input of large woody debris has been eliminated in the upper tidal floodplain.

Riverine sediment transport to the estuary, an important process affecting the quantity and quality of estuarine habitat for salmon, is correlated with peak river flows. It is impossible to separate the effects of flow regulation and irrigation withdrawal precisely from climatic variability. However, it is estimated that the corresponding change in annual average sediment transport (at Vancouver, Washington) for 1945–1999 flows has been about 50–60% of the 19th century (1858–1899) virgin sediment transport. The reduction in sands and gravels is higher (>70% of predevelopment) than for silts and clays.

In addition to peak spring-freshet flow and sediment-transport changes, the frequency in river-flow cycles is highly altered by the hydroelectric system's peaking cycle. Low frequency variations with periods between approximately two years and six months have been suppressed, and high frequency variations with periods of a week or less have been accentuated.

We conclude that the hydrological changes in the basin have caused a fundamental shift in the physical state of the Columbia River ecosystem. The member/vagrant hypothesis implies that such changes, including stabilization of river flows and elimination of overbank flooding, may have significant consequences for salmon populations, whose migration and rearing behaviors have adapted to historical patterns of hydrologic variability.

Estuarine Habitat Opportunity

We evaluated a two-dimensional numerical circulation model as a tool for understanding the dynamics of habitat opportunity for juvenile salmon and the potential effects of anthropogenic changes in the estuary that affect these dynamics. The model simulated changes in the occurrence and distribution of shallow-water, low-velocity habitat during predevelopment (1880) and modern (1997–1999) periods. Predevelopment and modern river flows and estuarine bathymetry were used to simulate and compare the habitat opportunity (total hours that "suitable habitat" occur in a one-month simulation period) for salmon in the historical and present estuary. "Suitable habitat" for juvenile salmon was operationally defined using two physical criteria: areas with water depths ranging from 0.1 to 2 m and areas with water velocities less than 0.3 m^3s^{-1}.

Results showed that availability of suitable habitat varies significantly within the estuary in response primarily to bathymetry but also to tides and river flows.

Seasonal and interannual variability also is very significant, particularly in the upriver, tidal-freshwater mainstem region and upper-estuary peripheral bays, where habitat opportunity is reduced during freshet months. Based on meeting the velocity criterion in model simulations, habitat opportunity under modern river flows and estuarine bathymetry has generally declined in the upriver, tidal-freshwater mainstem region and the upper-estuary peripheral bays (Cathlamet and Grays), while it has not changed dramatically in the lower regions of the estuary.

Model simulations of habitat opportunity based on the depth criterion, however, provide different results. Simulated depth regimes across the estuary suggest that habitat opportunity under modern flows and bathymetry has increased relative to historical conditions, except in the upper tidal-freshwater region. Yet limitations in the representation of modern bathymetry in the hydrodynamic model reduce confidence in the model simulation results based on the depth criterion.

Moreover, estimates based on the velocity criterion appear much less sensitive to model uncertainties than those based on the depth criterion. Since our level of confidence in the simulation results varies for each criterion, the modern and historical habitat opportunity based on the depth and velocity criteria combined cannot be interpreted now. Furthermore, because peripheral wetlands that were historically diked and filled are not well represented in the predevelopment bathymetry, the simulations may underestimate predevelopment habitat opportunity to an unknown degree.

Overall, model simulations have revealed several important features relating river flow and bathymetry to habitat opportunity:

- First, the results suggest that habitat opportunity in some regions of the predevelopment estuary was more resilient to increasing river flows than it is in the modern estuary. Resilience in this context refers to a reduced rate of change (slope) when correlating hours of habitat opportunity with river flow. This result was evident only in the upriver, tidal-freshwater mainstem region (above the main body of the lower estuary) and the upper-estuary peripheral bays (Cathlamet and Grays).
- Second, in the model simulations, estuarine bathymetry largely determined habitat availability as defined by the velocity and depth criteria described above. In addition, simulations of habitat opportunity under predevelopment bathymetry but with modern flows again suggested that bathymetric changes and habitat loss may be more influential in changing habitat opportunity than flow regulation.
- Third, seasonal changes in habitat opportunity have shifted between historical and modern conditions. Minimum habitat opportunity in the estuary is associated with freshets that now occur earlier in the year than they did in the late 1800s. The impact of advancing the period of minimum habitat opportunity for juvenile salmon is unknown.

These characterizations of change in shallow-water habitat are preliminary and must be viewed cautiously. Model predictions have not been empirically validated in regions without instrumentation, including the important shallow-water environments of Cathlamet Bay. Moreover, inadequacies in the modern bathymetric data affect habitat opportunity estimates, and substantial shoreline wetland and floodplain habitat lost to diking and filling are not fully incorporated in the simulations.

Although preliminary, these results demonstrate that simulation modeling can provide useful insights into the physical dynamics of the estuary and may help to identify the relevant constituents of salmon “habitat.” The model also predicts temporal and spatial changes in habitat opportunity that the member/vagrant hypothesis suggests could be significant to salmon diversity and resilience.

Estuarine Habitat Capacity

The productive capacity of the estuary has likely declined over the past century through the combined effects of diking and filling of shallow-water habitats, shifts from a macrodetritus-based to a microdetritus-based food web, and effects of introduced species. Loss of approximately 65% of the tidal marshes and swamps that existed in the estuary prior to 1870, combined with the loss of 12% of deepwater area, has contributed to a 12–20% reduction in the estuary’s tidal prism.

The absolute change in habitat area does not necessarily capture changes in habitat quality. For instance, while the dramatic loss of emergent and forested wetlands in the estuary has likely impacted foraging resources, the area of shallows and flats actually increased 7% between 1870 and 1980, which would have provided some additional foraging habitat. We have no means to objectively quantify the ecological effects of this habitat tradeoff because of the lack of historical data on the flora and fauna of these habitats.

Although a substantial decline in wetland primary production and associated macrodetritus for the estuarine food web is implied by direct loss of emergent, forested, and other wetland rearing areas, reduced macrodetrital input to the food web may have been supplanted to some degree by an increase in microdetritus from upriver sources. The increase is principally in the form of phytoplankton production from the hydropower and flood-control reservoirs.

The modern food web, however, does not support the same diversity of salmon life history types that occurred historically. The present microdetritus-based food web, which is centralized in the highly productive estuarine turbidity maximum region of the estuary, largely supports a pelagic food web that may contribute only indirectly to larger, yearling salmon.

Significant changes in the modern estuarine community through species introductions have not been assessed. However, the Asian bivalve, *Corbicula fluminea*, has expanded far into the lower mainstem reservoirs and tributary basins since its introduction into the estuary in 1938. *Pseudodiaptomus inopinus,* a calanoid copepod also introduced from Asia, has appeared prominently in the estuary since 1980, and American shad (*Alosa sapidissima*) has grown to a substantial population in the Columbia River since its introduction in 1885–1886.

Fifteen other nonindigenous fishes are now common in the estuary. The specific impacts on the estuarine ecosystem or on juvenile salmon in particular from any of these populations are speculative. However, given the tremendous abundance of *C. fluminea* and American shad (peak Bonneville Dam passage counts of 3×10^6), it is not unreasonable to expect that their consumption rates may have significantly modified the estuarine food web.

Predation on juvenile salmon in the estuary by piscivorous fishes, marine mammals, and birds has always been a mortality factor. Yet there are no data to compare historical and modern predation rates or predator populations. Several unique predator populations, including Caspian terns, have increased significantly in recent decades and could constitute potential limiting factors on juvenile salmon survival. A major limitation of contemporary predation studies is that predator consumption may be substantially affected by changes in salmon migration behavior associated with hatchery rearing and release programs.

Many of the changes in biological production processes that have occurred in the Columbia River estuary may be explained substantially by physical modifications that have altered the habitat landscape. These results lend further support to the member/vagrant hypothesis, which emphasizes the important role of physical and geographic factors (e.g., habitat opportunity) in shaping the dynamics and diversity of marine populations. These underlying physical linkages to estuarine production processes must be understood if salmon recovery programs are to treat the ultimate causes rather than the proximal symptoms of population decline.

Change in Juvenile Salmon Life History, Growth, and Estuarine Residence

The member/vagrant hypothesis predicts that the many biological and physical changes observed in the estuary could diminish salmon performance (e.g., growth, foraging success, and life history diversity) relative to historic conditions. We compared results of historical and contemporary fish surveys to assess change in the potential use of estuarine habitats by salmon based on these factors:

1) life history diversity of subyearling, ocean-type Chinook salmon,
2) periods of estuarine residence, and
3) growth and size characteristics.

Our analyses indicate that the population structure and life history diversity of subyearling Chinook salmon have been simplified significantly since the early 1900s. Reflecting the variability in emergence timing, migration distances, and growth rates among populations throughout the watershed, juvenile Chinook historically migrated to the estuary during much of the year and resided there for various time periods before migrating to the ocean.

In the predevelopment period, subyearling Chinook entered the estuary as fry in May and again as fry and fingerlings between July and August. Based on scale analyses, fish that resided in the estuary between June and July demonstrated rapid and substantial increases in mean length. To account for this average growth, many subyearling salmon would have resided in the estuary for as long as several months.

In contrast, contemporary patterns of estuarine use suggest that life history diversity of Chinook salmon has declined. Most data from modern fish collection are from marked, hatchery-reared fish, sampled predominantly along mainstem channels.

Relative to historical descriptions of Chinook salmon fry and fingerlings, modern fish enter the estuary considerably later (by at least two weeks), in pulses that coincide with hatchery releases, in a smaller range of fish sizes, and with a more homogeneous size distribution. Smaller subyearlings historically present during early fall are lacking in modern fish collections.

Unlike the historical continuum of rearing behaviors for juvenile Chinook salmon, three principal life history types are now dominant in the basin: subyearling migrants that rear in natal streams, subyearling migrants that rear in natal streams or main rivers or both, and a group of yearling migrants. Thus, the analyses suggest that ocean-type Chinook salmon with estuarine-rearing life histories are now substantially reduced in importance relative to their historical levels.

Our interpretations of historical and contemporary estuarine life histories and habitat use by juvenile salmon are limited by lack of systematic surveys in the estuary. Yet despite the many data deficiencies, the uniform sizes and rapid migrations of present-day salmon compared with those found at a nearby site in 1916 are consistent with the patterns expected from our conceptual framework based on the changes that have occurred throughout the Columbia River basin during the past 80 years, including:

- extinction of some salmon runs,
- loss of river reaches and shallow, estuarine habitats,
- flow modifications that have dampened established disturbance regimes and altered estuarine habitat,
- intensive harvest and other selection pressures, and
- hatchery programs that release large batches of similarly sized juveniles over a short period.

Synthesis: Review of the Conceptual Framework

We conclude that the member/vagrant hypothesis provides a valid framework for understanding the Columbia River estuary's contribution to the dynamics and diversity of salmon populations. Key assumptions of the hypothesis are supported by evidence that:

- salmon populations and life histories in the Columbia River basin are geographically structured,
- salmon performance in the estuary is directly linked to processes and conditions upriver, and
- "spatial losses"—factors that sever the linkages between salmon behavior and estuarine habitat—have played a significant role in population decline.

The member/vagrant hypothesis underscores the estuary's contribution to life history diversity and the geographic structure of salmon populations throughout the Columbia River basin. It argues that salmon recovery programs should be designed to expand habitat opportunities and the breadth of salmon life histories in the basin rather than simply targeting the few populations and life history types that have come to dominate salmon production under currently degraded habitat conditions and intensive hatchery programs.

The member/vagrant hypothesis provides the foundation for a new research agenda, including studies needed to reconstruct historic estuarine habitats and salmon life histories as a benchmark for setting restoration goals. It also emphasizes the need for broad, ecosystem-scale planning to reestablish estuarine-riverine habitat linkages that allow for the full expression of life history traits characteristic of each salmon population.

The member/vagrant hypothesis does not define a minimum quantity of habitat necessary to achieve population viability and, contrary to traditional production-based management approaches, argues that a single optimum condition for salmon production does not exist. Instead it emphasizes restoring flexibility to the ecosystem and its salmon populations by expanding habitat opportunities and life history diversity. We conclude that the member/vagrant hypothesis, while largely conceptual rather than prescriptive, promotes understanding of processes and linkages that will move the Columbia River ecosystem in a more favorable direction toward population persistence.

Acknowledgments

The authors are deeply indebted to Willis Horton Rich (1885–1972), whose 1920 study "Early history and seaward migration of Chinook salmon in the Columbia and Sacramento rivers" provided important historical data in this technical memorandum. Rich was a pioneer in the study of Pacific salmon migrations and life cycles, setting the foundation for generations of future biologists. His research demonstrated that juvenile Chinook salmon migrated through the mainstem Columbia River throughout the year, which he attributed to the movements of many independent populations distributed throughout the basin. From tagging studies with colleagues at the Bureau of Fisheries, Rich further demonstrated that spring and fall migrations of Chinook salmon were not random events but were inherited traits. Rich was among the first to recognize that the return of salmon to their natal streams creates a complex structure of isolated, self-sustaining populations within species. He proposed a revolutionary approach to salmon management based on the conservation of local populations within their native habitats. Rich resigned as director of the Bureau of Fisheries Pacific Fishery Investigations in 1930 to become a full professor at Stanford University and was named the first chief of research for the Oregon Fish Commission in 1937. In the 1940s, Rich and several other biologists with the U.S. Fish and Wildlife Service faced the daunting task of designing a fisheries conservation program to mitigate for proposed Columbia Basin hydroelectric development, including 40 dams, many on the mainstem Columbia and Snake rivers.

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Abbreviations and Acronyms

ADCIRC – Advanced Circulation model
BPA – Bonneville Power Administration
CORIE – Columbia River Estuary Evaluating System
CREDDP – Columbia River Data Development Program
ENSO – El Niño Southern Oscillation
ESA – Endangered Species Act
ETM – estuarine turbidity maximum
ESU – evolutionary significant units
FL – fork length
GIS – Geographic Information System
Ls – salinity intrusion length
mt – metric ton or metric tons
NMFS – National Marine Fisheries Service
NRC – National Research Council
NPPC – Northwest Power Planning Council
PDO – Pacific Decadal Oscillation
PIT – passive integrated transponder
Q_R – river flow
RKm – river kilometers
SWHA – shallow-water habitat area
USACE – U.S. Army Corps of Engineers
USGS – U.S. Geological Survey

Introduction

In the late 18th century, the entrance to the "Great River of the West" was expected to provide a Northwest Passage across the American continent and an inland highway for transpacific trade. The long-awaited Northwest Passage, however, repeatedly eluded European maritime explorers. Based on the currents and discolored water encountered near shore, Spanish explorer Bruno de Heceta believed he had found the continental passageway in 1775, but de Heceta did not attempt to enter the river he called the Rio San Roque. He was soon followed by an armada of unsuccessful Britons. James Cook tried three times to find the river, including a final attempt in 1778, when he sailed past the Columbia River mouth during the night.

A decade later, John Meares could not see beyond the long wall of surf and concluded that no river existed. He proclaimed his displeasure by dubbing the inlet Deception Bay and the rocky cape at its northern end Cape Disappointment (its present name). On 27 April 1792, George Vancouver discounted signs of discolored water as "some streams falling into the bay," and continued sailing northward past the river entrance. Finally, a few weeks later, American Robert Gray sailed the *Columbia Rediva* across the bar at Cape Disappointment and into the mouth of the Great River (Egan 1990, Dietrich 1995).

Difficult as the river was to find, its strategic importance was never in doubt. Gray verified the Columbia River's commercial potential; his first official acts included trade with the Chinook natives—a nail for two salmon (*Salmonidae)*, two nails for a beaver (*Castor canadensis*) skin, and a sheet of copper for four otter (*Enhydra lutris*) pelts. Gray not only redrew the regional map, but in symbolic exchanges of two of the river's principal assets—furs and salmon—he ushered in new and far-reaching economies that would forever reshape the Columbia River ecosystem. Along the 15 miles he ventured upstream, Gray collected more than 3,000 otter pelts that he sold in China (Egan 1990, Detrich 1995).

Although the commercial importance of the Columbia River estuary was immediately obvious, the natural economy of its murky waters remains as elusive today as its entry was to early explorers. The vast river network of the Columbia Basin drains an area about the size of Texas and funnels through a narrow tidal reach at the mouth in a roiling slurry of freshwater and saltwater, sediments, and organisms. From this narrow constriction of a few miles across its mouth, the Columbia River shoots a powerful jet of river water into the North Pacific, a plume that can be traced 1,040 km southward to San Francisco, California.

If the entrance to the mighty river was difficult to discover, how much more so will be the intricate physical and biotic interactions at its ocean juncture? It is not surprising that interest in the estuary the past 200 years has centered on practical uses and resources rather than on the obscure ecological interrelationships that support them. Yet crises have a way of exposing hidden obstructions and redirecting the focus. The rapid decline of Pacific salmon

(*Oncorhynchus* spp.) has expanded the need to explore the ecological depths of the Great River's estuary. This technical memorandum is part of that exploration.

In the past several decades, the Columbia Basin's bountiful populations of Pacific salmon have diminished to a small fraction of their former diversity and abundance. Numerous populations have declined or become extinct as a consequence of industrialized fisheries, habitat loss, hydropower development, and salmon hatchery programs. Since 1991, 13 Columbia River salmon stocks have been added to the list of threatened or endangered species under the U.S. Endangered Species Act (ESA). While traditional environmental assessments often have focused on habitat changes upriver, including the loss of spawning and rearing area following construction of large hydroelectric dams, questions are being raised about the estuary's role in the salmon's decline and potential recovery.

One analysis proposes that small survival improvements when spring and summer Chinook salmon (*O. tshawytscha)* enter the estuary and ocean could yield some of the most significant population increases (Kareiva et al. 2000). The need to better understand the effects of the Columbia River estuary and plume on salmon populations was recognized in recent policy changes governing salmon recovery programs throughout the basin.

On 12 September 1996, Congress amended the Pacific Northwest Electric Power Planning and Conservation Act of 1980 to include a section that requires the Northwest Power Planning Council (NPPC) to "consider the impact of ocean conditions on fish and wildlife populations" when recommending hydropower mitigation projects for the Columbia River basin. This new amendment to the Power Act applies directly to anadromous fish populations, particularly Pacific salmon and steelhead (*O. mykiss*), which have continued their precipitous decline despite decades of effort to mitigate effects of harvest and hydroelectric development in the basin. This legislation also focused attention on the estuary, which provides important rearing habitat for juvenile salmon during their seaward migration and is impacted by ocean conditions at the mouth and hydropower development upstream.

Concerns about the estuary and ocean represent a departure from previous management policy in the Columbia River basin. Earlier restoration had focused almost exclusively on the freshwater phase of the salmon life cycle, even though salmon spend most of their lives at sea. Recent research has shown that decades-long shifts in climatic and oceanic conditions can produce fluctuations in salmon production across the entire North Pacific Ocean (Francis and Sibley 1991, Beamish and Bouillon 1993, Mantua et al. 1997). Such natural variability must be taken into account to develop appropriate recovery goals, actions, and expectations for Columbia River salmon.

Legislation that requires a resource manager to look beyond freshwater recognizes that marine, estuarine, and riverine environments are components of an extended salmonid ecosystem and cannot be treated independently (ISG 2000, Williams in press, Bisbal and McConnaha 1998). While it is impossible to control fluctuations in the North Pacific, hydroelectric development and other upriver alterations affect the estuarine and nearshore coastal habitats of salmon, and the health and diversity of salmonids that enter the ocean. Ultimately these factors may decide whether salmon from the Columbia Basin can realize the full productive potential of the ocean under any particular set of environmental conditions. In response to the legislative mandate to consider the ocean, the NPPC recommended two management strategies:

1) improve estuarine and nearshore habitat conditions, which have been adversely affected by local habitat changes and upriver management activities, and
2) preserve the diversity of life history characteristics in salmon, which allows populations to withstand environmental fluctuations (NPPC 1997).

The NPPC also recommended several research initiatives to improve the understanding of ocean effects on fish and wildlife management activities, including "a synthesis of what is known about the impacts of the construction and operation of the Columbia River hydroelectric system on the hydrology, habitats, and ecology of the Columbia River estuary and river plume and opportunities for management actions related to this understanding" (NPPC 1998).

In 1999 the National Marine Fisheries Service (NMFS) formed an estuarine research team to evaluate whether existing information is adequate to:

- interpret effects of the hydroelectric system on the Columbia River estuary as outlined in the NPPC research initiative, and
- support NPPC strategies concerning ocean viability such as improvement of estuarine and nearshore habitats and preservation of life history diversity in salmon.

This technical memorandum summarizes the assessment of conditions in the Columbia River estuary. The purpose is to offer management recommendations for improving estuarine conditions for salmon or to identify research that will be needed before management changes can be defined or both. This report focuses on four key questions about salmon in the Columbia River estuary:

1. What habitats and processes support native salmon populations during the estuarine phase of their life cycle?
2. Have changes to the estuary had a significant role in salmon decline?
3. What have been the impacts of flow regulation on the hydrology, habitat, and biological interactions in the estuarine ecosystem?
4. What estuarine conditions are necessary to maintain salmonid diversity in the Columbia River basin?

To address these questions this technical memorandum summarizes existing knowledge about the estuarine requirements of juvenile salmon, reconstructs historical changes in estuarine conditions, and uses simulation modeling to predict changes in rearing opportunities for juvenile salmon. The historical analysis considers changes in the estuarine environment and changes in the salmon populations that may determine whether these fish can fully use the habitats that are available. The emphasis is on subyearling fish, primarily juvenile fall Chinook salmon, because these are considered the most estuarine dependent and because less information is available for other species or Columbia River age classes. The analyses are designed to distinguish effects of flow regulation from bathymetric and other changes and to put these anthropogenic effects in the context of long-term climatic fluctuations.

This technical memorandum summarizes the available information regarding salmon habitats and life histories in the Columbia River estuary. In lieu of empirical data depicting long-term trends or changes in estuarine habitat use by salmon, we evaluate whether simulation modeling can provide a means to characterize historic and present rearing opportunities for subyearling salmon. This approach relies on literature values for estuarine water depths and velocities generally preferred by subyearling salmon. The simulations characterize salmon-habitat opportunity as the total number of hours that the proposed shallow-water or low velocity criteria are met under selected tidal, river-flow, and bathymetric conditions.

The first two sections of this technical memorandum establish the context for the evaluation, including a review of historical changes in the basin that have affected salmon populations and estuarine conditions, and the conceptual approach upon which the specific analyses and interpretations are based.

The subsequent sections describe the results of our analyses, including:

- hydrologic and climatic fluctuations in the Columbia River basin for the past 140 years and the effects of hydroelectric operations and other management activities on established flow patterns,
- preliminary model simulations to compare availability of estuarine habitat for salmon under historic and present bathymetric and flow conditions,
- the status of knowledge about ecological changes within the estuary that have affected habitat quality and rearing capacity for salmon, and
- the performance of salmon in the estuary using indicators of growth and life history.

We review the results in the context of our conceptual approach and conclude with recommendations for future estuarine management and research.

The depth of this estuarine exploration is limited, because little data have been collected on juvenile salmon and their habitat use in the estuary. Although the habitat modeling demonstrated the sensitivity of the ecosystem to changes in flow and bathymetry, the results are preliminary, because existing bathymetric data are inadequate to resolve habitat response to these changes.

This technical memorandum is more than a compilation of facts and conclusions about the estuary; it also proposes an alternative framework for interpreting the effects of estuarine habitat change on Columbia River salmon populations. Traditional assumptions about the factors regulating salmon populations have undermined understanding of the estuary and have played a prominent role in salmon decline (Lichatowich 1999). We believe an alternative way of thinking about salmon, therefore, is a prerequisite for their recovery. This review is as much an illustration of how such a framework of ideas can be applied to the Columbia River estuary as it is a presentation of results based on that framework.

Estuarine Development History and Salmon Decline

Estuary Description

With a watershed of roughly 660,500 square kilometers (km^2) encompassing seven states, two Canadian provinces, and two major continental mountain ranges (Cascades and Rockies), the Columbia River is the second largest river in the United States. The river and estuary are dominant features in the circulation of the northeast Pacific Ocean with a mean annual discharge at the mouth of approximately 5,500 cubic meters per second (m^3s^{-1}). We define the Columbia River estuary (Figure 1) to include the free-flowing waters that are influenced by oceanic tides: a reach spanning 235 river kilometers (RKm) from the mouth to the base of Bonneville Dam. Relative to juvenile salmon migration along the estuarine gradient, this system includes three physiographic subsystems:

- the tidal freshwater portion or fluvial region (Simenstad et al. 1990a) from Bonneville Dam to the maximum upstream extent of salinity intrusion (≈55 RKm from the entrance),
- the brackish-mesohaline region above the open expanse of the main estuary (≈30–55 RKm from the entrance), and
- the broad, euryhaline region in the lower 30 RKm of the estuary.

Ecological studies in the estuary during the early 1980s further partitioned the euryhaline region into seven subareas (Simenstad et al. 1990a):

1) entrance,
2) Trestle and Baker bays in Oregon,
3) Youngs Bay in Oregon,
4) estuarine channels,
5) mid-estuary shoals of the estuarine mixing zone,
6) Grays Bay in Washington, and
7) Cathlamet Bay in Oregon.

This lower estuarine area encompasses a complex network of main, distributary, and dendritic tidal channels; non-vegetated shoals; emergent and forested wetlands; and extensive mudflats in peripheral bays. Approximately 26,550 (≈ 71.2%) of the 37,289 hectares in the estuarine region are composed of shallow-water habitats (6 m or less relative to mean lower low water). Except in peripheral bays, where silt and clay sediments dominate, most of the estuary's sediments are composed of sand. More detailed descriptions of the river flow and sediment

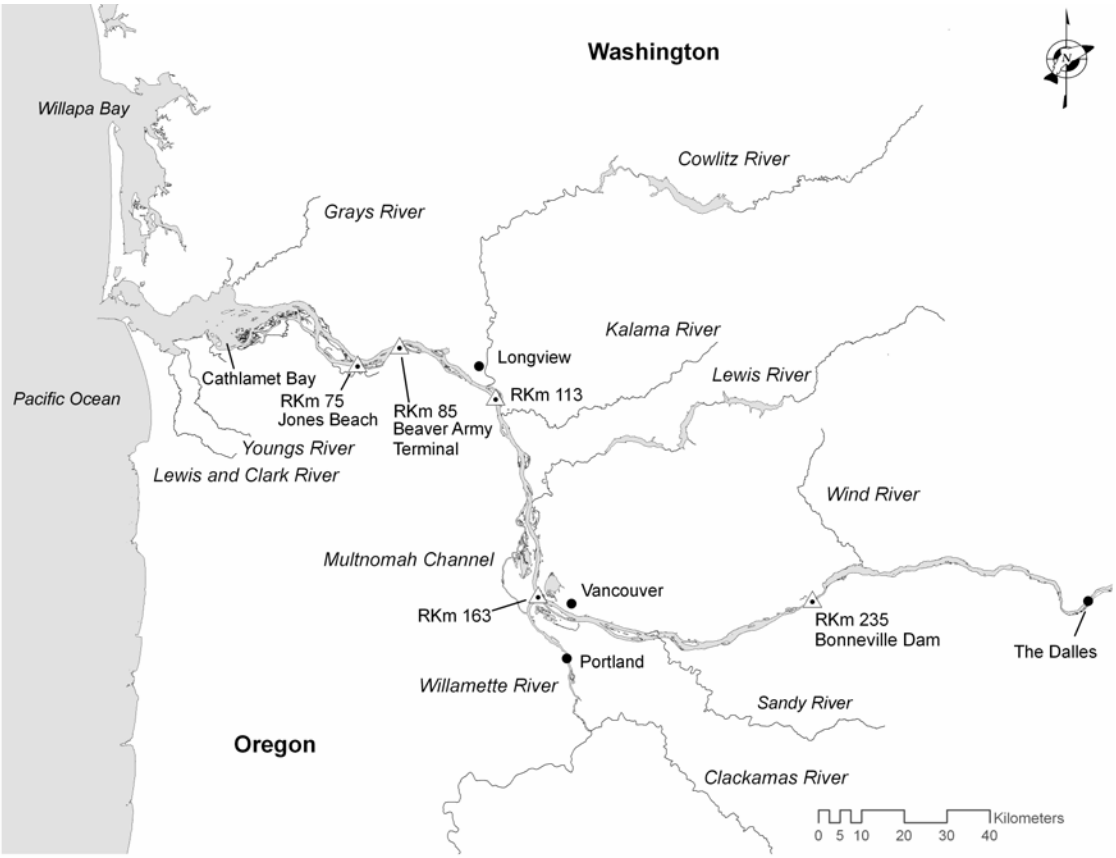

Figure 1. The tidal influence of the Columbia River extends upstream from its mouth at the Pacific Ocean to the Bonneville Dam (RKm 235).

transported through the estuary can be found in the "Changes in Hydrological Conditions" section (page 47).

The low salinity surface water of the Columbia River plume forms an offshore extension and fourth physiographic province of the estuary. The plume affects surface density gradients and the physical properties of coastal waters, and it may be an important feature influencing biological production processes and potential rearing opportunities for seaward migrating salmonids. For the purposes of this technical memorandum, however, we limit our assessment to the eastern portion of the estuary encompassing the three physiographic provinces described above.

Estuarine Requirements of Juvenile Salmon

All anadromous salmonids that survive to reproduce pass through estuaries at least twice during their life cycle: first as juveniles en route to the Pacific Ocean and then as adults when they return to spawn in their natal streams. In the estuary, all seaward migrating juveniles must make the transition from shallow, freshwater, lotic environments to a deep, salty, open ocean within a period of days to months.

Estuaries are often presumed to offer three advantages to juvenile salmon for making this transition:

1) a productive feeding area capable of sustaining increased growth rates,
2) a temporary refuge from marine predators, and
3) a physiological transition zone where juvenile fish can gradually acclimate to saltwater (Simenstad et al. 1982, Thorpe 1994).

Pacific salmon species and populations have evolved diverse strategies for using all available freshwater and estuarine nursery habitats within a river basin (Healey 1982, Groot and Margolis 1991). The duration of estuarine residence varies considerably among species and sizes of juvenile salmon. Salmonids that rear in freshwater for a year or more before migrating downstream (some Chinook, sockeye [*O. nerka*], and coho [*O. kisutch*]) are believed to move rapidly through the estuary and may not spend substantial periods adapting to saltwater before ocean entry. These are frequently referred to as “stream-type” fish.

However, subyearling migrants that enter the estuary as fry or fingerlings, so-called “ocean-type” salmon, exhibit a wide range of residence periods depending on the species. Pink salmon (*O. gorbuscha*) exhibit little estuarine rearing; chum salmon (*O. keta*) stay in estuaries for days to weeks; and subyearling Chinook salmon may remain for several months (Thorpe 1994).

Chinook salmon, which have the greatest diversity of juvenile life histories among all Pacific salmon (Healey 1991, Wissmar and Simenstad 1998), have the most varied patterns of estuarine use. Healey (1982) proposed that Chinook salmon are the most estuarine-dependent of salmonid species since virtually all life history types spend time feeding and growing in estuaries, a physiological transition zone where juvenile fish can gradually acclimate to saltwater (Simenstad et al. 1982, Thorpe 1994).

Regardless of the residence times of individual fish, juvenile salmon may occur in the estuary all year, as different species, size classes, and life history types continually move downstream and enter tidal waters from multiple upstream sources. Peak estuarine migration periods vary among and within species, suggesting that different life history strategies may provide a mechanism for partitioning limited estuarine habitats (Myers and Horton 1982). The varied juvenile life histories in Chinook salmon are manifest in the wide range of sizes and times of estuarine entry (Rich 1920, Healey 1982). In the Columbia River estuary, subyearling Chinook salmon are most abundant from May through September but are present all year (Rich 1920, McCabe et al. 1986). Rich (1920) first reported that for each Chinook brood in the Columbia River, juvenile migrations span an 18-month period, including fry that migrate soon after emerging in December and yearlings that do not leave until late in their second spring.

The size of Chinook salmon at the time of ocean entry may reflect the various alternative rearing options available to juveniles before they make the complete transition to an ocean environment. Large numbers of Chinook enter estuaries in southern British Columbia, Canada, as fry and leave at relatively small sizes (60–70 millimeters fork length [mm FL]) at about the time subyearling Chinook smolts migrate downstream (Healey 1982). In the Nanaimo River system on the east coast of Vancouver Island, subyearling smolts reside in the outer estuary in

June and July and some remain year-round. The earlier disappearance of most Chinook from southern British Columbia estuaries may reflect the availability of protected habitat along the complex archipelago of the Strait of Georgia (Healey 1982). Although fewer fry migrants have been reported in coastal Oregon estuaries (e.g., Reimers 1973, Myers 1980), many subyearling Chinook often use estuaries through the summer and into early autumn before they migrate at relatively large sizes. Estuaries along the open Oregon coastline thus may be particularly important as shelter for juvenile salmon that must migrate directly into an open ocean environment.

Many studies indicate that the movements of juvenile salmon and their habitat use within estuaries are size related. Small Chinook and chum salmon (subyearling) fry usually occupy shallow, nearshore habitats, including salt marshes, tidal creeks, and intertidal flats (Levy and Northcote 1982 , Myers and Horton 1982, Simenstad et al. 1982, Levings et al. 1986). As subyearling salmon grow to fingerling and smolt stages, their distribution typically shifts toward deeper habitats farther away from the shoreline (Healey 1982, 1991, Myers and Horton 1982). Although the specific size transitions may vary, numerous estuarine studies have found juvenile salmon distributed along a habitat continuum: juvenile Chinook and chum less than 50–60 mm FL occur primarily in shallow water (e.g., <1 m); fish 60–100 mm FL are found in slightly deeper habitats (shoals, distributary channels); and fish greater than 100 mm FL may be found in deep- and shallow-water habitats. This direct relationship between size and habitat depth tends to break down during hours of darkness, when schooling fry or fingerlings often disperse from shore (Schreiner 1977, Kjelson et al. 1982, Bax 1983, Healey 1991, Salo 1991).

The distribution of juvenile salmon in the Columbia River estuary is consistent with this notion of differential habitat use based on fish size. McCabe et al. (1986) reported that subyearling Chinook in shallow intertidal habitats of the Columbia River estuary were smaller than subyearlings captured in deeper pelagic areas. Large yearling migrants may spend relatively little time in shallow estuarine habitats. A 1980–1981 survey of the estuary found most yearling Chinook salmon at deeper channel sites rather than at nearshore intertidal sites (Bottom et al. 1984).

Rapid changes in salinity gradients, water depths, and the accessibility of habitats impose important ecological and energetic constraints that salmon do not experience in freshwater: salmon must continually adjust their habitat distribution, particularly in shallow-water areas, with twice-daily tidal fluctuations and seasonal variations in river flow. The landscape distribution of habitats throughout an estuary may be important in juvenile salmon adaptation to tidal and seasonal changes. In most estuaries, salmon fry move twice daily from low tide refuge areas at the junction of major and minor channels to salt marsh habitats at high tide and back again (Healey 1982, Levy and Northcote 1982). Chum and Chinook salmon fry remain in marshes of the Fraser River estuary in British Columbia for an average of 11 and 30 days, respectively (Levy and Northcote 1982). Thus access to suitable low tide refugia located immediately adjacent to marsh habitats may be an important factor in salmon production and survival as juveniles traverse the estuarine landscape.

Appropriate sequences of habitat distributed across the entire estuarine salinity gradient also may be necessary to support the seasonal migrations of juvenile salmon (Simenstad et al. 2000b). Throughout their migration and rearing period in estuaries, subyearling migrants traverse a continuum of salinities, depths, and water velocities as they gradually grow and migrate from upper tidewater to lower estuary and from shallow nearshore to deeper offshore areas. For species (e.g. chum and Chinook salmon) that remain in the estuary for extended periods, a broad spectrum of habitat types may be needed to satisfy feeding and refuge requirements within each salinity zone. But even large coho smolts may require a sequence of habitat types to allow for extended holding periods during their relatively brief stay in the estuary. Radio-tagged coho salmon in the Gray's Harbor estuary in Washington interspersed periods of passive downstream movement in strong currents with periods of holding in low velocity habitats (Moser et al. 1991). Because the parr-smolt transformation is a key period when salmon gather the olfactory information they need for successful homing, and because the cues for imprinting may depend upon environmental gradients experienced during migrations and physiological changes, habitat sequences at a landscape scale may be important even for those salmonids that move through the estuary relatively quickly (Dittman et al. 1996).

Marsh habitats, tidal creeks, and associated dendritic channel networks may be particularly important to small subyearling salmonids as areas of high secondary production of insect and other invertebrate prey; sources and sinks for detritus; and potential refuge from predators afforded by complex habitat structure, including sinuous channels, overhanging vegetation, and undercut banks (Levy and Northcote 1982, McIvor and Odum 1988, Gray et al. 2002). Salmonid production in Northwest estuaries is supported largely by detrital food chains through a variety of animals that live in or near the estuary bottom (Healey 1979, 1982). Habitats that produce or retain detritus are particularly important. Detrital sources vary along the estuarine tidal gradient but include emergent vegetation in tidal wetlands, low intertidal and subtidal eelgrass, macro-algal beds, and epibenthic algae (Naiman and Sibert 1979, Sherwood et al. 1990). Historically, before the Columbia River was isolated from its floodplain, considerable organic matter was probably imported into the estuary during seasonal freshets and winter flooding events.

In the Columbia River estuary, low velocity, peripheral bay habitats (e.g., Baker, Youngs, and Grays bays) and the estuarine turbidity maximum (ETM) in the mid-estuary are regions where organic matter is concentrated. It is also where invertebrate prey production and fish and macro-invertebrate feeding are elevated relative to other estuarine locations (Bottom and Jones 1990, Jones et al. 1990, Simenstad et al. 1990a). Loss of historic wetlands and macro-algal habitats (e.g., mud and sand flats) within the estuary and enhanced phytoplankton production in impoundments upriver may have shifted estuarine food chains from macrodetrital to microdetrital sources (Sherwood et al. 1990). Such changes would likely benefit food chains supporting pelagic-feeding fishes such as northern anchovy (*Engraulis mordax*), longfin smelt (*Spirinchus thaleichthys*), surf smelt (*Hypomesus pretiosus*), Pacific herring (*Clupea harengus pallasi*), and American shad (*Alosa sapidissima*) with commensurate loss of food webs supporting epibenthic-feeding fishes such as juvenile salmon.

Historical Change in Salmon Populations and Estuarine Habitats

To understand patterns of habitat use within the estuary, we must account for changes at all life stages that shape the structure and life histories of salmon populations. Salmon species composition, abundances, sizes, and migration periods in the estuary are linked to changes upriver or in the ocean that determine which populations and juvenile life history types survive to enter tidewater. The biological characteristics and density of salmon in the estuary may be influenced by these multiple factors:

- selective harvest in ocean and river fisheries,
- adult access to upriver spawning and rearing habitats,
- rearing and release practices in hatcheries, and
- climate and river flow.

Historic changes to the Columbia River populations and habitats (see Appendix A, page 229), which may affect salmon rearing conditions in the estuary, are detailed elsewhere (NRC 1996, Lichatowich 1999, ISG 2000, Williams in press) and briefly summarized in the following subsections.

Population Decline

Prior to European settlement, the Columbia River system sustained annual adult returns from 11–16 × 10^6 salmon[1] of which Native North Americans likely harvested between 4.6–6.3 × 10^6 fish (Craig and Hacker 1940, NPPC 1986). All five species of Pacific salmon were historically present in the Columbia River, although pink salmon abundance was always quite low (Heard 1991, NRC 1996). Less than 190,000 km^2 (<45%) of the more than 422,000 km^2 of habitat originally available for salmon spawning and rearing is now accessible (NRC 1996, [Figure 2]). In the Snake River, ocean-type Chinook salmon now occupy approximately 17% of the historic habitat (Hassemer et al. 1997). Virtually none of the historic salmon habitat in the portion of the Columbia River in Canada is accessible. Through habitat loss and other changes, present natural production of salmon in the Columbia River basin has been reduced to approximately 12% of historic levels. Since 1991 sustained population declines have resulted in listings of 13 salmonid stocks as threatened or endangered under the ESA (Table 1).

Different species and life history types of salmon occur in somewhat different spawning and rearing areas of the Columbia River basin (Figure 3 and Figure 4). Thus the geographic patterns of habitat and population loss on the landscape may determine the particular species and life history types represented in the estuary. Scientific observations of salmon, however, occurred after habitat losses and harvest effects had altered biological patterns in the Columbia River basin. Therefore the understanding of salmon life history, including the generalizations in this report, may be substantially oversimplified.

Chum salmon are confined principally to the lower Columbia River tributaries, excluding the Willamette River drainage in Oregon; coho salmon once occupied all tributaries west of the Cascade Mountains and larger tributary systems (e.g., the Yakima, Wenatchee, Entiat, Methow and Spokane rivers in Washington; and the Grand Ronde River in Oregon) on the eastern side; sockeye salmon primarily use lake systems high in the watershed; steelhead are found throughout the major headwater systems; and three to four types of Chinook salmon occupy the mainstem channel and primary tributaries (Fulton 1970).

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[1] Other estimates of total run-sizes are often significantly lower, such as 7.5 × 10^6 (Chapman 1986) and 6.2 × 10^6 (PFMC 1979).

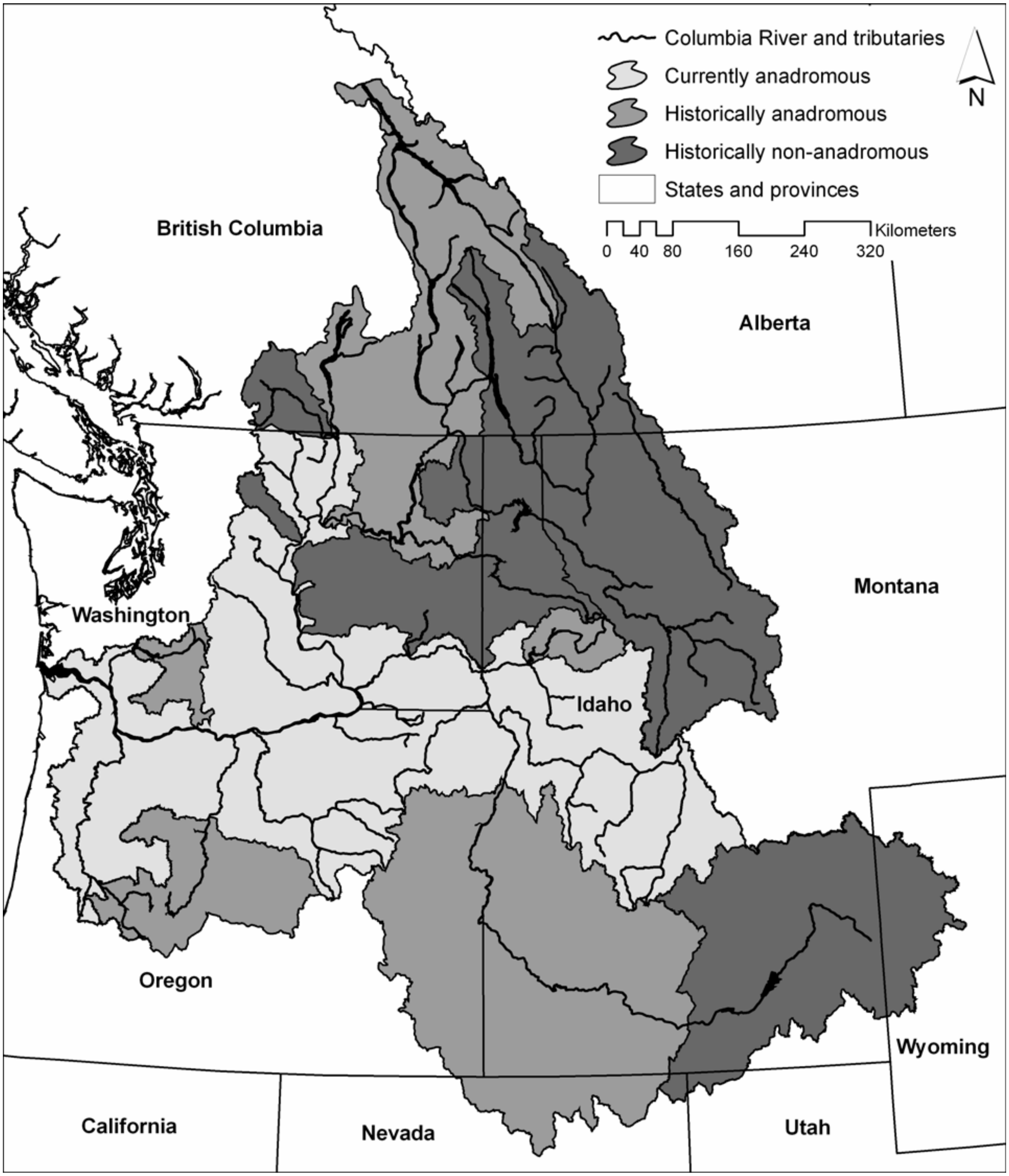

Figure 2. Current and historical distribution of anadromous salmonids in the Columbia River basin.

Table 1. Listings and proposed listings of Columbia River salmonids under the ESA. Listings include various evolutionary significant units (ESU) within each species as designated by the NMFS.

Species	ESA status	ESU	Date
Coho salmon	Listed	Lower Columbia River/ Southwest Washington	Threatened: June 28, 2005
Chinook salmon	Listed	Snake River fall run	Threatened: April 1992
		Snake River spring/summer run	Threatened: April 1992
		Lower Columbia River	Threatened: March 1999
		Upper Willamette River	Threatened: March 1999
		Upper Columbia River spring run	Endangered: March 1999
Chum salmon	Listed	Columbia River	Threatened: March 1999
Sockeye salmon	Listed	Snake River	Endangered: November 1991
Steelhead	Listed	Upper Columbia River ESU	Endangered: August 1997
		Snake River basin	Threatened: August 1997
		Lower Columbia River	Threatened: March 1998
		Upper Willamette	Threatened: March 1999
		Middle Columbia River	Threatened: March 1999

Chinook salmon were once distributed throughout the basin, but distinct stocks or run types[2] occupied somewhat discrete regions (Figure 5). Ocean-type, fall-run Chinook were concentrated in the lower watersheds west of the Cascades and in the mainstem Columbia east of the Cascades. Stream-type, spring-run Chinook extended throughout the Columbia River basin but were most commonly found in the Snake River watershed. Summer-run Chinook spawned and reared primarily in mainstem reaches of the Columbia east of the Cascades, particularly in the Snake River drainages.

Factors of Decline

Rapid growth of European civilization in the Pacific Northwest brought dramatic changes to Columbia River salmon and their riverine and estuarine habitats. For the past century, the overall trend in salmon abundance has been one of decline, reflecting a myriad of factors that undermined the natural productive capacity of the Columbia River basin (see Appendix A, page 229). The principal causes of salmon decline are discussed in the following subsections (NRC 1996).

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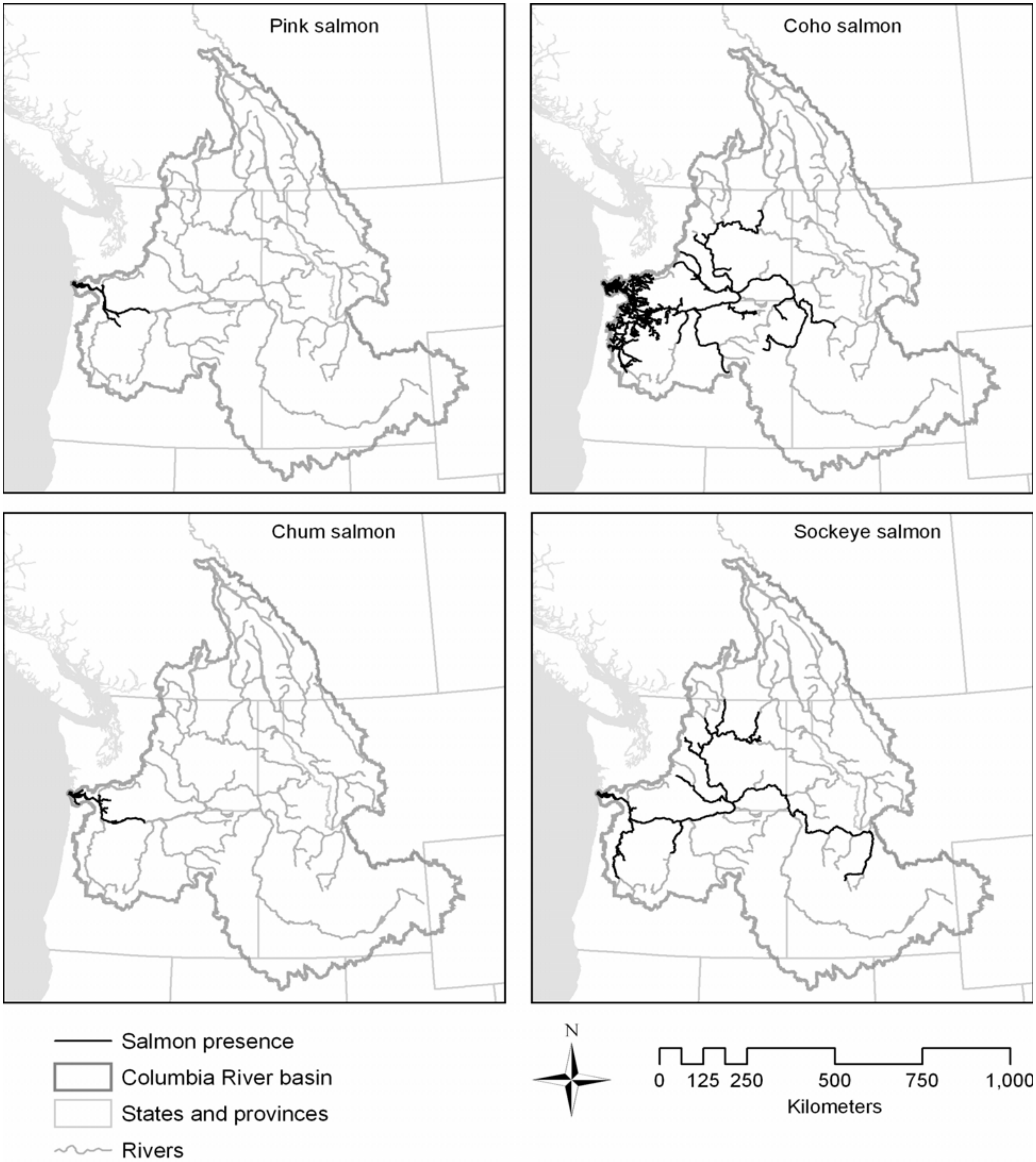
[2] It is important when considering Columbia River salmon population and life history structure to understand that our present-day characterization of fall-run, spring-run, and summer-run stocks was the product of a terminology derived from the commercial fishery rather than a scientific differentiation of independent breeding populations. Recent genetic typing may improve our understanding of this complex stock structure.



Pink salmon

Coho salmon

Chum salmon

Sockeye salmon

Figure 3. Present distribution of pink, coho, chum, and sockeye salmon in the Columbia River basin. Salmon presence from StreamNet (2003).

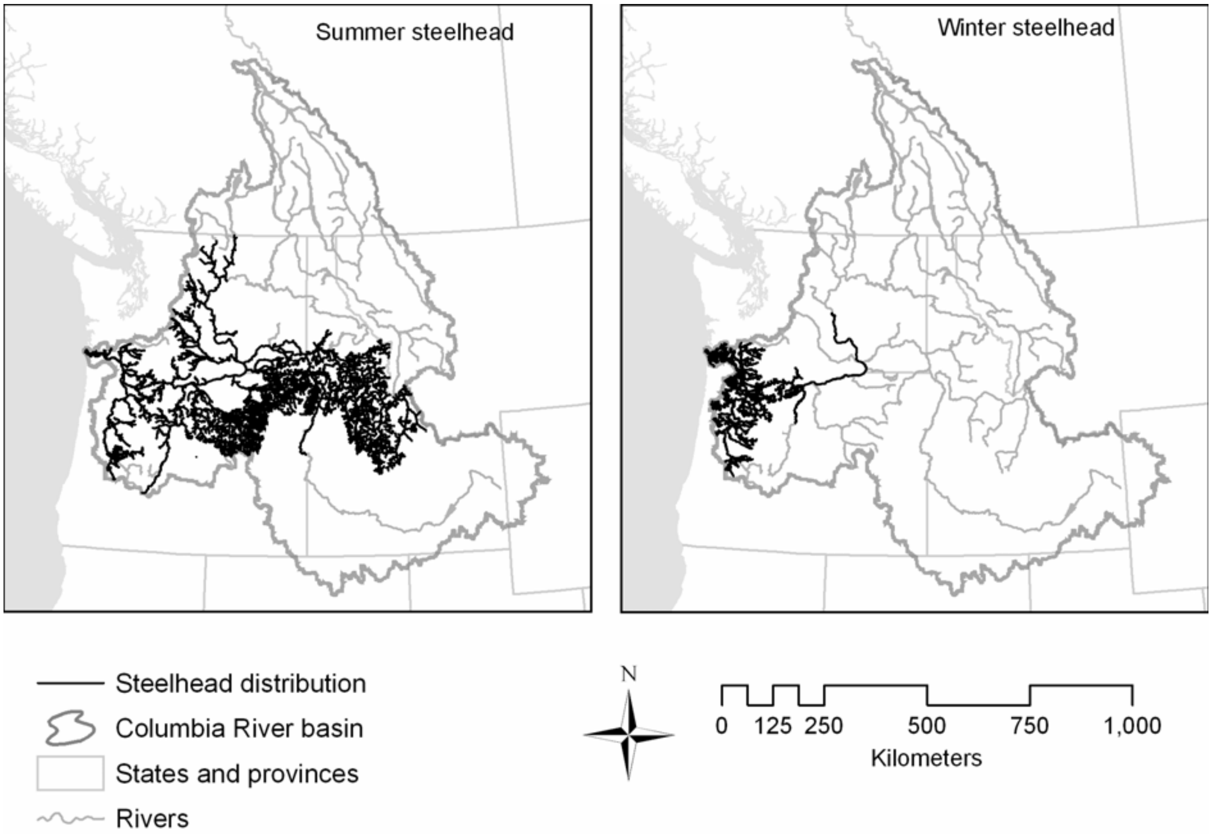


Figure 4. Present distribution of summer and winter steelhead in the Columbia River basin. Steelhead presence from StreamNet (2003).

Salmon harvest

Fisheries for Columbia River salmon became well established within four decades after de Heceta's 1775 discovery of the river's outlet to the Pacific Ocean. During a similar period of fishing activity, targeted salmon stocks (i.e., spring Chinook) were already showing signs of depression. Commercial harvest of adult salmon began in about 1818 with packing of salmon as a salted or pickled product, but it increased dramatically with the advent of commercial canning in 1866.

Harvest intensity increased rapidly in response to cannery demand starting in 1866 for an eight-year period (Lichatowich et al. 1996). Commercial fishermen initially targeted spring-run Chinook, considered the superior canning variety. By 1890 the concentrated harvest of these fish in the estuary and the lower river was blamed for the dramatic reduction in the number of adults returning to spawn in the Snake River basin (Evermann 1895). Salmon populations had declined throughout the Columbia River system by 1911.

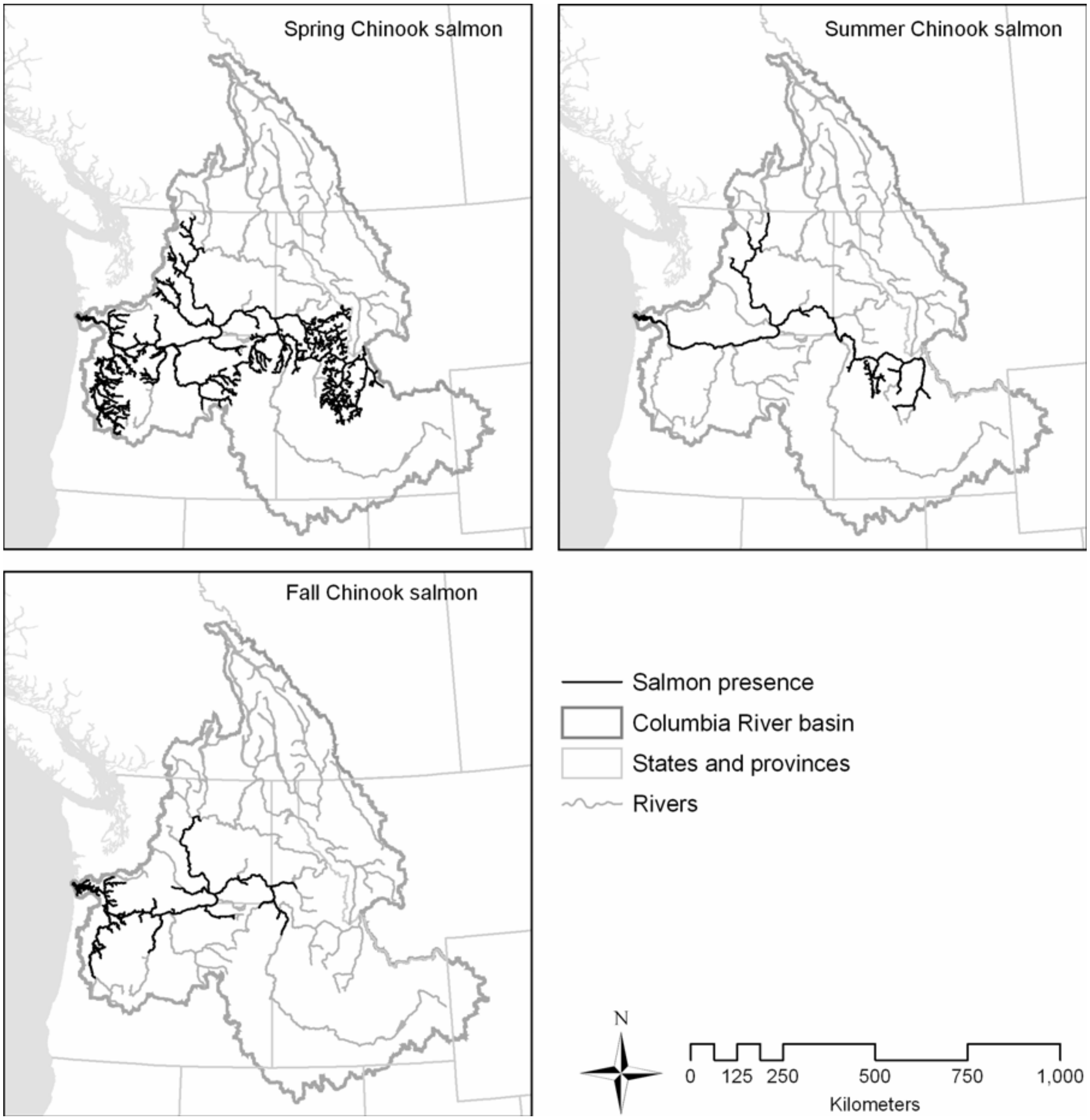


Figure 5. Present distribution of spring-, summer-, and fall-run Chinook salmon in the Columbia River basin. Salmon presence from StreamNet (2003).

Changes in freshwater habitat

Although irrigation in the basin began about the same time as the development of industrial salmon fisheries, it did not increase substantially until after implementation of the Reclamation Act of 1902, which stimulated expansion of irrigated lands from 2,000 km^2 to nearly 40×10^6 km^2 today (NPPC 1986, NRC 1996). Yet surface water withdrawal did not accelerate until after World War II, principally in the mid-1960s, with technological advances and the availability of inexpensive electrical power. Irrigation not only decreased stream flow, but it also became a sink for migrating juvenile salmon that were diverted into irrigation canals and stranded in farmers' fields. As early as 1890, state fish commissioners reported substantial losses of juvenile salmon in irrigation networks in Eastern Oregon (OSBFC 1890).

Extensive streambed and water modifications began to eliminate upriver spawning, rearing, and migratory habitats for salmon by the late 1800s. As early as 1894 mining in the Snake River watershed destroyed Chinook spawning beds and was credited with the collapse of a popular American Indian fishing site (Taylor 1999). Habitat loss increased after the turn of the century, because of logging and other intensive land uses such as cattle grazing. Even prior to 1900 some practices damaging to salmon spawning and rearing habitat were prevalent, including removal of large woody debris from streams and the operation of splash dams (Sedell and Luchessa 1982, NRC 1996).

Dam construction throughout the Columbia River basin also has depleted salmon populations, and it accounts for much of the present-day reduction in historic salmon distribution (Figure 2). Chinook salmon populations from the upper Columbia River basin in Canada, middle Snake River basin and above in Idaho, and the greater part of the Deschutes River basin in Oregon have been extinct for at least 40 years because of dams built without fish passage capabilities. There are 23 major hydropower and flood control dams on the mainstem Columbia and Snake rivers today, and more than 300 smaller dams distributed on tributaries throughout the U.S. portion of the watershed (Figure 6).

Salmon hatcheries

Resource managers responded to declining Columbia River harvests in the mid-1890s by building salmon hatcheries, promoted as a means to boost salmon production to avoid the need for harvest regulations, and to improve on nature by using efficient technology to increase freshwater survival (Baird 1875, NRC 1996, Taylor 1999).

Despite poor accounting for their performance and a general decline in support for hatcheries in the 1930s and 1940s, hatchery production expanded substantially in later years, stimulated by a new promise that artificial production could mitigate for the deleterious effects of dams and irrigation development (NRC 1996). Ultimately more than 80 hatcheries were constructed in the basin (Figure 6).

Hatchery adults now comprise more than 95% of the coho, 70% of the spring Chinook, about 80% of the summer Chinook, more than 50% of the fall Chinook, and about 70% of the steelhead returning to the Columbia River (CBFWA 1990, Genovese and Emmett 1997).

Hatchery influence on Chinook populations is now greatest for fall Chinook in the middle and lower Columbia River subbasins (>85% of total juvenile salmon production [Genovese and Emmett 1997]), and for spring and summer Chinook in the Snake and Salmon rivers subbasins (90–100% of the total production). More than 75% of the Chinook salmon in the Deschutes, John Day and upper Columbia rivers subbasins still results from natural production. On average, most hatchery fall Chinook are released as fed fry, and 70% of the chum salmon now produced in the lower Columbia River subbasin are released from hatcheries as fed fry or fingerlings.

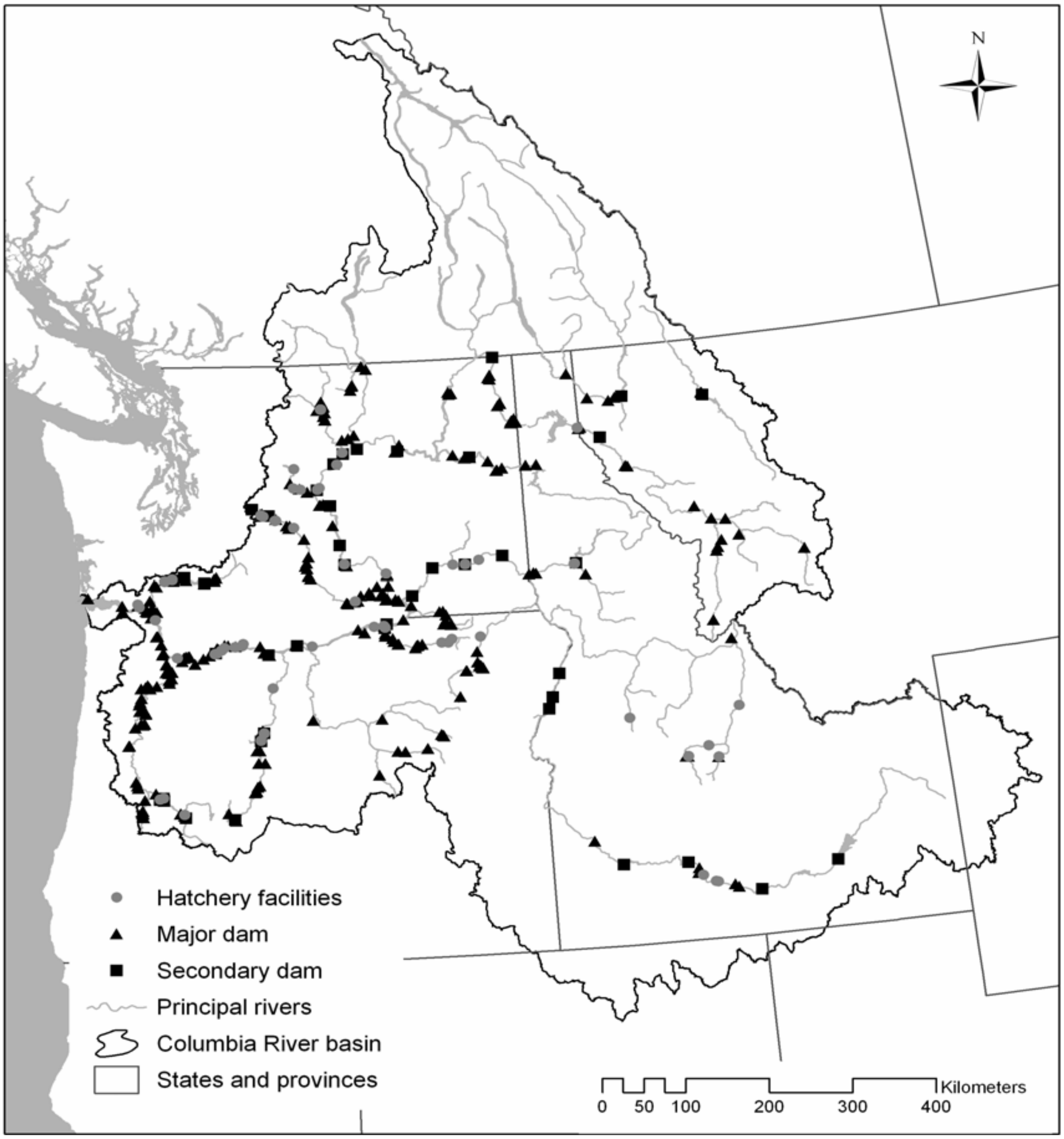


Figure 6. Present distribution of salmon hatcheries and mainstem and secondary dams (StreamNet 2003) along rivers and streams of the Columbia River basin.

Intensive hatchery programs have had multiple effects on natural salmon production in the Columbia River basin and on the recovery potential of at-risk populations (NRC 1996). Among these effects are reduced genetic diversity, competition between hatchery and naturally produced salmon, and depletion of wild populations in mixed stock fisheries. Loss of genetic and life history diversity through large-scale hatchery production (Reisenbichler 1997) could be an important factor determining patterns of estuarine habitat use and the overall performance of juvenile salmon in the estuary.

Changes in the estuary

Most loss and degradation of habitat within the Columbia River estuary occurred after the 1880s. Following a century of diking and filling activity, only 35% of the former area of marsh and swamp habitat remained in the estuary in 1980 (Thomas 1983). However, this is a gross estimate of the total habitat loss based on historical surveys. Other qualitative changes in physical conditions also may have had important effects on the salmon rearing capacity of the estuary.

Shoreline armoring and construction of structures over water, channel dredging and removal of large woody debris, channelization by pile dikes and other structures, and discharge of pollutants have significantly modified estuarine habitats. The effects of such alterations on either juvenile or adult salmon rarely have been assessed.

Early channel dredging and hatchery production began to alter estuarine conditions in the second half of the 19th century; it was not until the 20th century that channelization and filling removed considerable amounts of estuarine habitat, and hydropower and irrigation developments significantly altered river flows. The salmon harvest was already in a state of decline (Taylor 1999). Although there were at least 174 dams in the basin by 1936 (see Appendix A, page 229), many of the mainstem dams that would comprise the Columbia River hydropower system were not completed until the 1950s. Significant coordinated flow modifications did not occur until the late 1960s (Sherwood et al. 1984).

Climate variability

Development activities in the Columbia River watershed and estuary were superimposed on a background of natural environmental changes, including substantial variations in climate, precipitation, and river flow (see the "Changes in Hydrological Conditions section, page 47). Climatic fluctuations often accounted for a greater degree of variation than those resulting from human interventions. Prior to 1910, spring freshets recorded at The Dalles, Oregon, often exceeded 20×10^3 m^3s^{-1}, and winter flood flows in the Willamette River exceeded 5×10^3 m^3s^{-1} (18 of 60 years). Spring and winter peaks decreased dramatically thereafter, especially during the drought years of the 1930s (Sherwood et al. 1984).

Although the magnitudes of these changes are impressive and suggest major shifts in riverine and estuarine disturbance regimes, Columbia River salmon stocks have withstood such disturbances for millennia (Chatters et al. 1995). Long-term productivity and the resilience of salmon species are the result of diverse life history strategies that have evolved in a highly variable environment (Healey 1991, Healey and Prince 1995). A primary concern of recent salmon declines is whether habitat changes and reduced salmon diversity in the Columbia River basin have severely undermined the capacity of populations to withstand large fluctuations, particularly major changes in long-established patterns of precipitation, temperature, and stream flow that some predictions suggest could accompany future global warming (Mantua et al. 1997).

Institutional fragmentation

A vast number of governmental agencies, management jurisdictions, and laws have been created that directly affect salmon populations and their habitats. The net result is a fragmented and often-conflicting array of resource-management programs with jurisdictional boundaries and land ownerships that do not coincide with the spatial distributions of salmonid species with anadromous life cycles. One analysis of the Columbia River basin estimated that a Chinook salmon hatched in the Lochsa River in Idaho crosses at least 17 separate international, federal, state, and tribal jurisdictions during the later stages of its life cycle (Wilkenson 1992). The National Research Council (NRC 1996) concluded that fragmentation of institutional responsibilities and a mismatch between the spatial scales of salmon habitats and management jurisdictions severely undermine salmon conservation throughout the Pacific Northwest.

In conclusion

The cumulative effects of upstream developments on salmon-rearing conditions in the estuary are poorly understood. Yet the combined influences of river-flow regulation and industrial hatchery production are noteworthy because of their direct impact on salmon life histories or on the disturbance processes to which those life histories have adapted. Hydroelectric development now largely regulates the timing and magnitude of river flows, with potential effects on salmon migrations and on circulation processes and habitat conditions in the estuary. Hatchery programs now regulate the size, time of arrival, distribution, and rearing periods of most salmonids in the estuary. Thus upriver controls placed on water and on fish have fundamental linkages to salmon production in the estuary.

History of Research in the Columbia River Estuary

Scientific and engineering research on the Columbia River estuary has been modest given the river's social, cultural, economic, and strategic importance to the region (see Appendix A, page 229). As described in Simenstad et al. (1990a), studies prior to 1980 tended to be fragmented, focusing on applied issues and target resources rather than on a broader ecological understanding of the interactions among the estuary's physical environment, chemical structure, and biota. Early estuarine research projects were either engineering studies required to construct the jetty or navigation channels, or to compensate for depleted salmon runs. Infrequent biological studies of the timing and distribution of juvenile salmon began as early as 1914–1916, when Rich conducted his first studies in the estuary (Rich 1920). With few exceptions, including McIssac's (1990) research on the Lewis River in Washington, fall Chinook studies have not attempted to link population structure and performance of upriver salmon stocks to their utilization of the estuary.

The richest source of information on juvenile salmon and their habitats in the estuary originates from studies conducted since the early 1970s by NMFS biologists stationed at the Point Adams Research Station at Hammond, Oregon. These efforts evaluated migration behavior of juvenile salmon and steelhead transported around hydropower dams (Dawley et al. 1978, 1981, 1985, and 1986), dredging and dredged-material disposal impacts, particularly on the benthic biota (Durkin et al. 1979 and 1981, Emmett et al. 1986, Hinton et al. 1990, 1992a, and 1992b), or stranding of juvenile salmon on beaches from ship traffic (Durkin et al.1977).

Results for salmon, crab, and estuarine habitat characteristics in the Columbia River estuary were ultimately reported in scientific literature (Durkin 1982, McCabe et al. 1983).

Scientific investigations of the spatial and temporal distributions of nutrients and biota and the supporting ecology of the Columbia River estuary are described by Haertel and Osterberg (1967) and Haertel et al. (1969). These complemented the results of comprehensive studies sponsored by the U.S. Atomic Energy Commission to determine the fate of radionuclides from the Hanford Nuclear Reservation in Washington (Pruter and Alverson 1972), providing a description of the estuary's physical and biological conditions.

The Columbia River Data Development Program (CREDDP) studies during 1979–1980 (Simenstad et al. 1990a) represent the most noteworthy interdisciplinary examination of the estuary to date. The CREDDP investigations provided the first description of fundamental estuarine processes, including sediment accretion (shoaling) and productivity and trophic structure (Bottom and Jones 1990, Jay et al.1990, Jay and Smith 1990, Jones et al. 1990, Sherwood and Creager 1990, Small et al. 1990). The CREDDP studies also modeled estuary-scale circulation patterns (Hamilton 1990), quantified organic matter transfer through the estuarine food web (Simenstad et al. 1990b), and assessed effects of historical change on the estuarine ecosystem (Sherwood et al. 1990). Results of the CREDDP studies are summarized in a synthesis report by Simenstad et al. (1984) and in a series of articles in Progress in Oceanography (1990, Vol. 25).

The CREDDP studies supported the first comprehensive recovery of marked juvenile salmon below the tidal-freshwater reaches of the lower river. Not since the early scale analyses of Rich (1920) had studies linked estuarine residence times to early freshwater life histories (McIssac 1990). The CREDDP studies also documented changes in the estuary from the May 1980 eruption of Mount St. Helens, including declines in juvenile salmon foraging efficiency (Emmett 1982, Emmett et al. 1991). The CREDDP studies inspired more than a decade of ecological research on the estuarine turbidity maxima by the National Science Foundation's Land-Margin Ecosystem Research Program (Simenstad et al. 1994).

Despite these efforts, fundamental studies evaluating the links between juvenile salmon and estuarine conditions in the Columbia River generally are lacking. Notably missing is information delineating:

1) specific (especially shallow-water) habitats used by salmon during rearing and outmigration through the estuary,
2) effects of physicochemical and biological conditions on estuarine residence times, growth, or survival of juvenile salmon,
3) food-chain relationships (feeding and predation) among juvenile salmon, invertebrate prey, and vertebrate predators, and
4) differences in these estuarine habitat needs and ecological relationships among salmon species, life history types, and source populations.

Until the basic biological data have been assembled, biologists can only speculate about the dependence of juvenile salmon on estuarine habitats or the relative impacts of historic changes in river flow, estuarine bathymetry, or ecological interactions in the estuary.

A Conceptual Framework for Evaluating Estuarine Habitat Conditions

Introduction

The lack of information about the esturary's role in salmon life history is surprising considering the importance of the Columbia River basin to the salmon. The estuary is a huge system; however, with some exceptions (Levy and Northcote 1982), present understanding of salmonid ecology comes from studies of small estuaries undertaken within recent decades (Reimers 1973, Healey 1980, Tallman and Healey 1994). While this research provides information about wild fry and subyearlings, much of what is known about salmon in the Columbia River estuary is based on larger yearling or fed subyearling fish released from hatcheries. As a result we lack information about the specific life-support functions of the Columbia River estuary for salmon for two reasons:

1) ecological processes in much smaller estuaries may not apply directly to this large, river-dominated system, and
2) the behaviors of hatchery fish in the Columbia may not represent the estuarine needs of naturally produced salmonids.

Despite a few ecological surveys of fish assemblages and food chains (Haertel and Osterberg 1967, Bottom and Jones 1990), the estuarine life histories of diverse populations of salmon and the physical and biological processes that influence their estuarine habitats have rarely been investigated and are poorly understood.

What is or is not known about the estuarine requirements of Columbia River salmon reflect certain underlying principles and assumptions in traditional fishery management. These concepts set limits on the kinds of information that were collected and also determined how that information was interpreted (Sinclair and Solemdal 1988, Lichatowich et al. 1996, ISG 2000, Williams in press). Traditional lack of interest in the estuary resulted in part from assumptions about the factors that regulate salmon production.

Recent concerns about the estuary, including recommendations that led to this evaluation (NPPC 1997), suggest a fundamental change in the conceptual approach to salmon ecology. These concerns are reinforced by numerous listings of Columbia River salmon stocks under the ESA (Table 1), which emphasizes the importance of conserving biological diversity and the native ecosystems upon which it depends. It is important the scientific basis for these changing ideas be understood in order to develop a satisfactory framework for this evaluation.

Fisheries science developed from an agricultural perspective of resource management (Bottom 1997). This perspective supported a progressive conservation philosophy that emphasized efficient production of natural resources for the benefit of all people. Science provided the methods and technologies to increase production of natural resources, compensate for losses to development, and provide for an equitable distribution of resources among all users (Bottom 1997, ISG 2000, Williams in press). To meet these utilitarian goals, resource management programs relied on a framework of scientific ideas we might call "production thinking." This perspective measured success by the output of natural resources (e.g., pounds or numbers of salmon, angler days of use, etc.) and favored predictive methods and technologies to achieve production goals. Production thinking emphasized short-term changes in the abundance of salmon populations, which were defined arbitrarily as any geographic unit of management interest (e.g., river basin, state or nation). From a production viewpoint, the term "population" was an abstraction defined by a particular management need or question.

Recent mandates to improve estuarine conditions and to protect life history diversity in salmon (NPPC 1997) are derived from a different conceptual framework that was proposed explicitly to support salmon recovery programs in the Columbia River basin (ISG 2000, Williams in press). This framework emphasizes continuity of the chain of freshwater, estuarine, and marine habitats that support salmon life cycles; it requires information about the life histories and evolutionary adaptations of salmon to their natural environments; and it places salmon survival at any one life stage in the context of the animals' prospective success in navigating the entire habitat chain.

This long-term perspective is based on "population thinking," which defines populations as reproductively isolated and self-sustaining groups of animals within particular geographic areas (Mayr 1982, Sinclair 1988, Sinclair and Solemdal 1988). In contrast to the arbitrarily defined units of the production approach, this perspective views populations as functional reproductive units with distinct genetic and geographic characteristics (Kingsland 1995). Population thinking raises new questions, for example, about the geographic structure of populations on the landscape and the specific habitats that support them.

A primary challenge for this analysis was how to answer questions about estuarine habitats and salmon recovery that require a geographic and an evolutionary perspective (ISG 2000, Williams in press), when most of the available information has been collected and interpreted from a production view. To establish a conceptual framework appropriate for the objectives of this evaluation, the first step is to review the underlying assumptions applied to past salmon research and management in Northwest estuaries. We contrast ideas from estuarine studies that were based on production thinking to those based on population thinking. We then examine a theory of populations derived from marine fish ecology as a starting point for the conceptual approach and the specific analyses selected for this assessment.

Historical Perspectives on Salmon in Estuaries

Production Thinking in Estuarine Research

Although the traditional assumptions of fisheries management have received increased scrutiny in recent years (McEvoy 1986, Finlayson 1994, Lichatowich 1999, ISG 2000, Williams in press), the impact of these ideas on salmon research and management in estuaries has not been examined specifically. The lack of research interest in Northwest estuaries stems in part from long-held assumptions that populations are regulated by density-dependent interactions—biological factors such as predation, disease, or food competition—during the earliest and presumably most vulnerable stages of salmon life. These ideas focused attention on the freshwater habitats where salmon are most easily observed and where the sources of mortality can be controlled.

Salmon hatcheries, for example, developed from the assumption that adult abundance is limited by freshwater mortality, and that abundance increases in direct proportion to the number of additional eggs that survive when they are reared in a controlled environment (Lichatowich 1999). Theoretical models in population ecology and the concept of "maximum sustained yield" similarly assumed density-dependent control of salmon and developed equations to describe the apparent relationship between population size and the resulting number of recruits (e.g., Ricker 1948, Larkin 1977).

Salmon hatcheries and harvest models have had widespread appeal for two reasons.

1. They reinforced the fundamental economic view of fishery management (Bottom 1995, 1997).
2. They also met new standards of scientific legitimacy, as modern ecology actively shunned historical and descriptive explanations for the reductionist and predictive methods of the physical sciences (Kingsland 1995).

Both achieved this predictability by simply eliminating natural variation: hatcheries through technological control of the only variations assumed to be important (i.e., those in freshwater), and harvest models by averaging the apparent relationship between population size and recruitment over the period of observation (Cushing 1995). In both cases, the assumption that populations are regulated by a predictable, freshwater struggle for existence allowed fishery management to avoid the messier stages of the salmon life cycle that were more difficult to understand or control.

This is not to say that the estuarine life of salmon has been ignored altogether. But even when the estuary has been considered, management and research activities often extended to tide water the same agricultural ideas used to remove production constraints upriver. After the turn of the century, for example, state fish commissioners sought legislative support and later successfully established bounties for marine birds and mammals under the assumption that large numbers of estuarine predators constituted a significant "waste" of an economic resource and should be destroyed (Reed 1901). When hatchery technology had developed the means to rear salmon for extended periods and control most of their freshwater mortality, fishery managers looked for additional ways to protect their investment by eliminating other perceived threats immediately below the hatcheries.

In the late 1940s, Gharrett (1955) transferred groups of hatchery Chinook and coho fingerlings directly into the Nehalem River estuary in Oregon to test whether the procedure could be used to avoid instream competition with wild fish, predation during downstream migration, and the expense of holding subyearling fish in hatchery ponds until their second spring. A few decades later similar ideas were implemented on a larger scale when the Oregon State Game Commission constructed an estuarine impoundment for holding salmon fry in Lint Slough in the Alsea River estuary (Raynor and Garrison 1965, Garrison 1966, Holm 1969). By regulating tidal and river flows and trapping nutrient-rich ocean water in the shallow slough, fishery managers hoped that salmon would thrive on a rich estuarine prey base, eliminating hatchery food costs, increasing growth rates, and protecting fish from riverine and estuarine predators (Holm 1969, Bottom and Simenstad 2001).

Declining salmon runs in the late 1970s highlighted the failure of traditional hatchery operations to maintain or increase salmon returns and raised new questions about whether estuaries might be "bottlenecks" to production. Based on the apparent success of Japan's massive chum salmon production program, several large U.S. corporations developed ocean-ranching facilities with salmon release and recapture sites located near the mouths of several Oregon estuaries. Researchers began monitoring potential interactions between private hatchery and wild juveniles, concerned that hatchery-released fish might not migrate directly to sea and could compete with wild, estuarine-rearing salmonids (Nicholas et al. 1979, Myers and Horton 1982, Nicholas and Herring 1983, Nicholas and Lorz 1984). Some initiated "carrying capacity" studies to estimate the quantities of hatchery Chinook salmon that estuaries could support (Reimers et al. 1979, Nicholas and Downey 1983, Nicholas et al. 1984).

To test the estuary bottleneck theory, researchers conducted experiments to compare smolt survival of hatchery coho and Chinook salmon released in river and barged various distances offshore of the Columbia (Solazzi et al. 1991) and Fraser rivers estuaries (Macdonald et al. 1988, Levings et al. 1989). Reminiscent of the early experiments that moved fish to the estuary to eliminate potential in-river mortalities (Gharrett 1955, Raynor and Garrison 1965, Garrison 1966), these experiments tested whether salmon are "estuarine dependent" or whether survival could be increased if salmon simply avoided the estuary altogether.

Present research in the Columbia River estuary remains a downstream extension of upriver ideas to control salmon production and mitigate for hydropower-system effects. Some estuarine studies are designed around fish tagging technologies and the incidental availability of experimental groups of marked fish used to evaluate hatchery rearing practices, barging operations for transporting fish around dams, and the relationships between river flow and fish passage through the dams. The NMFS has maintained a monitoring site at Jones Beach (RKm 75) in Oregon to provide a tidewater recovery point below Bonneville Dam (RKm 235) where migration timing, travel times, and survival for various groups of marked salmon can be estimated to the upper estuary (Dawley et al. 1986). Ongoing research on salmon predation by Caspian terns (*Sterna caspia,* [Roby et al. 1998, Collis et al. 1999, USACE 1999, Ryan et al. 2001 and 2003]) similarly relies on estuarine recoveries of Passive Integrated Transponder (PIT) tags from fish marked upriver, extending to the estuary earlier concerns about fish predation below mainstem dams and in the reservoirs (Beamesderfer and Rieman 1988, Beamesderfer at al. 1990, Rieman and Beamesderfer 1990).

It is unclear, however, how the migrations, rearing requirements, or survival of estuarine salmonids should be interpreted from various upriver tagging studies. The probabilities of recapturing marked fish at Jones Beach or recovering tags at a Caspian tern colony in the lower estuary depend on the numbers and characteristics of individuals chosen for numerous upriver experimental groups. Marked fish do not represent the full diversity of sizes, geographic origins, or life histories of juvenile salmonids throughout the basin. Estimates of travel times or predation rates for marked fish may not apply to those of smaller subyearlings that are most likely to rear in the estuary for extended periods but are least likely to be tagged upriver.

Because the design of these studies is dictated by the sampling opportunities that are created by hatchery, tagging, and recapture technologies—opportunities that emphasize relatively large hatchery fish with yearling life histories—it is unlikely the results apply similarly to all juvenile life history types in the estuary. Results for tagged hatchery fish, even if the results did represent behaviors of the majority of individuals that are now produced in the Columbia River ecosystem, provide little information about the historical habitats or life history types that have been lost and that a successful recovery program ultimately may need to reestablish.

In summary, a common theme of production thinking in salmon management is the notion that estuaries, like rivers (Lichatowich 1999), are hazardous places. A primary goal of production-oriented research is to identify, eliminate, or avoid apparent ecological constraints, particularly any obvious predators or competitors in the estuary. This approach emphasizes the need to reduce estuarine mortality of juvenile salmon regardless of their geographic origins or life histories or whether any of the additional survivors would be destined to return as adults. Because it focuses on presumed threats to salmon, production thinking provides little or no information about the estuarine habitats and conditions that salmon need. Instead, the estuary is seen as a corridor through which a single, large, and undifferentiated mass of fish must confront predators before they can escape to the ocean. Among the many assumptions inherent to this view are the following:

- The factors that limit salmon production in estuaries are separable from conditions experienced during other life stages and can be treated independently.
- Estuaries have significant excess carrying capacity to accommodate large releases of hatchery fish (ISG 2000, Williams in press).
- Estuarine abundance of juvenile salmon is regulated top down by predators (or sometimes bottom up by competitors) through density-dependent processes.
- The number of adult salmon produced each year is a function of the rate of predation (or competition) that occurs in the estuary.
- To avoid predators or competitors and improve survival rates, salmon must move rapidly through the estuarine corridor.
- Adult returns will increase in proportion to the number of estuarine predators or competitors that are removed or otherwise prevented from interacting with salmon.

Population Thinking in Estuarine Research

Not all research in the Columbia River estuary has taken a strictly production-oriented view of salmon. The first significant study in the estuary (Rich 1920) was a descriptive survey to understand Chinook salmon biology and life history in the Columbia River basin. This survey began as an outgrowth of Gilbert's (1913) early studies of sockeye salmon in British Columbia rivers, where he devised methods for interpreting salmon life histories from the patterns of circuli recorded on their scales.

Rich's (1920) research was not an estuary study, per se; it was a survey of the periods of migration, sizes, and ages of juvenile salmon migrants as they moved through the main river and estuary toward the ocean. To interpret the migration behaviors he found in the estuary, Rich looked upstream. Despite a comparatively short period of spawning for Chinook salmon throughout the basin, Rich found young salmon of a wide variety of age-and size-classes moving downstream and through the estuary throughout the year. From the distinct rearing histories recorded on the salmon scales, he inferred that this continuous estuarine migration was the sum of many independent populations whose separate movements and rearing patterns reflected different climatic and environmental conditions across the basin. For fish that remained in brackish water, Rich also documented, from scale patterns, a significant increase in growth rate relative to growth in freshwater, suggesting improved rearing conditions in the estuary.

Rich's (1925 and 1927) continued research on adult salmon in the Columbia River basin provided much of the information he used to demonstrate that salmon indeed return to their home streams to spawn. He concluded that each salmon species is composed of a large number of local, self-perpetuating populations, whose behaviors are molded by the particular sets of conditions found in their spawning and nursery areas (Lichatowich 1999). These results contributed to Rich's (1939) ideas for an entirely new management approach that defined each population and its associated watershed as the fundamental unit of salmon conservation.

The population ideas that Rich (1939) developed from empirical observation defined a different kind of estuary from the one envisioned based on production thinking (Table 2). Rather than a simple corridor through which a single, homogeneous group of outmigrants move as rapidly as possible to avoid voracious predators, Rich's estuary was a complex nursery ground where a continuous stream of individuals from geographically discrete populations converged and remained for varying periods of time. From this perspective, diverse salmon rearing behaviors in the estuary became linked to habitats upriver where self-sustaining populations spawned and reared. Thus a fundamental implication of population thinking is that estuarine habitat use and salmon migration patterns may depend as much on the status of upriver habitats and source populations as on the environmental conditions within the estuary itself.

In the past few decades, population thinking has played a significant role in understanding the estuarine ecology of salmon, particularly in some smaller Northwest estuaries (Reimers 1973, Carl and Healey 1984, Healey 1982, Simenstad et al. 1982). Ironically these ideas have had little influence on research in the Columbia River estuary since the 1930s, despite the fact this system provided much of the early data from which population thinking and the entire stock concept of salmon conservation originally developed (Rich 1939 and Ricker 1972). By then hydroelectric and irrigation development in the Columbia Basin had shifted attention back to the more familiar production approach that emphasized the development of hatchery, fish bypass, and transportation systems to compensate for upriver habitat and population losses (Lichatowich 1999). Despite the implications of Rich's early population studies, and except for occasional concerns about estuarine predators and competitors, the expanding business of fish production had little interest in the estuary.

Table 2. Contrasting views of salmon conservation in estuaries based on production and population thinking.

	Production thinking	**Population thinking**
Goals	Efficiency, production	Resilience, reproduction
Population units	Arbitrarily defined	Biologically defined
Time frame	Short	Evolutionary
Objectives	Control survival and abundance	Conserve local populations and life history diversity
Estuary function	Corridor for a single, homogeneous group of salmon	Nursery area for many self-sustaining populations
Estuary management	Control predators, promote rapid salmon seaward migration	Protect habitats of diverse life history types

A Theory of Populations with Complex Life Cycles

Marine ecologists have become increasingly aware that species with complex life cycles—distinct developmental stages located in spatially discrete habitats—may be regulated by ecological processes coupled among different environments. Roughgarden et al. (1988) noted that marine rocky intertidal communities at some sites are regulated by adult interactions and competition for space, while at other sites distant ocean currents and upwelling processes control populations by limiting the larval supply. Thus traditional stock-recruitment approaches may not adequately describe the dynamics of marine populations with complex life cycles, whose transport or migrations link processes in distant habitats, and whose survival can be regulated by physical processes unrelated to population density.

The migrations of anadromous salmonids similarly integrate processes across vastly different aquatic environments. Research indicating that salmon production is regulated by large-scale shifts in the North Pacific Ocean and atmosphere (Francis and Sibley 1991, Beamish and Bouillon 1993, Mantua et al. 1997) contradicts traditional ideas that density-dependent interactions during the earliest life stages are sufficient to explain salmon variability. The role of density-independent processes in salmon production may be particularly important in the California Current region, which is considered a physically controlled ecosystem, wherein plankton assemblages and carrying capacities are regulated by ocean currents and upwelling events rather than biological interactions (McGowan and Walker 1993).

Climatic shifts in the North Pacific not only influence marine survival of salmon but also control processes at all other stages of the salmon life cycle by modifying flow and temperature conditions upriver and salinity gradients and sediment transport in estuaries (Greenland 1994, Melack et al. 1997). A framework for understanding salmon variability must account for freshwater, marine, and estuarine processes that are linked through salmon migrations.

One approach that may be useful for understanding the role of estuarine habitats for salmon is Sinclair's (1988) member/vagrant hypothesis, which proposes a set of general principles for understanding the dynamics of marine species with complex life cycles. Unlike the production focus of traditional fishery management, Sinclair's hypothesis uses population thinking to account for four characteristics of marine populations simultaneously:

1) differences between species in population richness,
2) the geographic patterns of populations within species,
3) control of absolute (e.g., mean) abundance, and
4) control of population variance.

The member/vagrant hypothesis provides a useful perspective for evaluating the specific needs of salmon within estuaries while placing the needs in context of the entire continuum of habitats needed to sustain salmon life cycles.

Population Pattern and Richness

The member/vagrant hypothesis states that the pattern and richness (diversity) of populations are determined by the number and location of geographic features where a species' life cycle can be brought to closure (Sinclair 1988). According to this idea, complex life cycles of marine populations have evolved in response to certain persistent features in the environment that allow sexually reproducing individuals to find a mate with a similar genome. Because membership in a population (e.g., successful reproduction) requires that individuals be in the right place at the right time, certain geographic features provide a predictable setting in which organisms of reproductive age can converge at an appropriate time in otherwise diffuse and dispersive aquatic environments.

Thus life histories of marine and anadromous species involve transport and migration behaviors that are linked to particular geographic features including streams, estuaries, offshore banks, currents, ocean gyres, and upwelling systems. Sinclair's hypothesis suggests that the number of geographic settings allowing a species to complete its life cycle successfully determines the number of its component populations.

According to this idea, marked differences in population richness among marine species are associated with the number of various egg and larval retention areas around which the life histories of populations have become adapted. The European eel (*Anguilla anguilla*, [Figure 7]), which consists of one panmictic population whose egg and larval retention area is the entire North Atlantic gyre (Sinclair 1988), are at the low end of the spectrum. The Atlantic herring (*Clupea harengus*), which consists of multiple populations that result from a series of discrete larval retention areas maintained within coastal embayments, estuaries, and certain tidal circulation features of open-ocean spawning grounds, are at the high end.

The most population-rich of Sinclair's examples is Atlantic salmon (*Salmo salar*), which, like Pacific salmon, have a diverse population structure defined by the number of streams and rivers flowing into the ocean and to which adults home for spawning. Precise homing allows even populations in adjacent streams to become isolated and adapted to local conditions

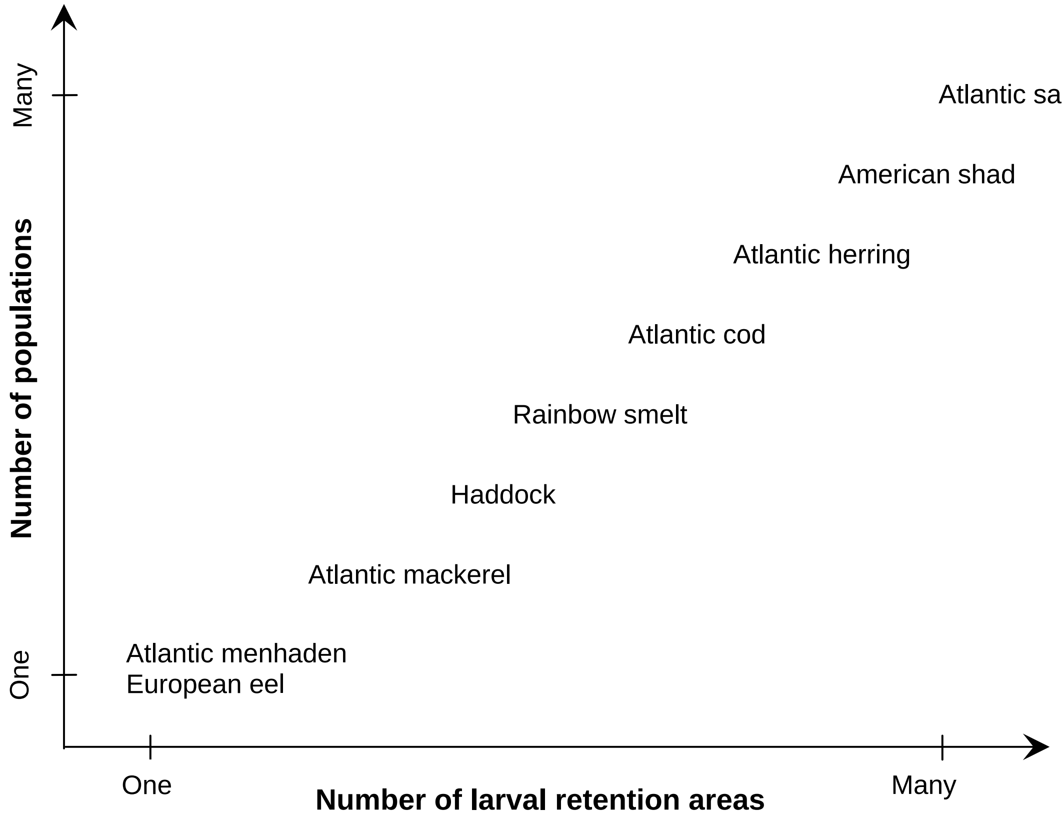


Figure 7. The continuum in population richness of selected anadromous and marine species in the northern Atlantic (adapted from Sinclair 1988).

(Miller and Brannon 1981, Carl and Healey 1984). Common to these examples is the segregation of early life stages among population groups and the interpopulation mixing during later stages. Differences among species in population richness are explained by this separation of populations during the early life stages based on the same specific geographic features to which adults home to reproduce.

A critical underpinning of the member/vagrant hypothesis is the interaction between physical geography and the behavior (e.g., life histories) of individuals that use various persistent features of aquatic systems to maintain membership in a population. The vertical migration behaviors of many zooplankton and pelagic stages of benthic invertebrates, for example, are adapted to the two-layered, estuarine tidal circulation that aids their retention in estuaries and minimizes individual losses from populations (Sinclair 1988).

Such interactions between physical geography and behavior similarly characterize the anadromous life cycles of Pacific salmon. Diverse salmon life histories that include broad variations in timing and size of seaward-migrating fish and periods of estuary residence represent alternative time/space solutions for completing anadromous life cycles within the overall distributional range and physiological constraints of each species. Distinctions in migration timing, size, and rearing periods are linked to fine-scale features within each aquatic environment (stream, river, estuary, and ocean) where salmon seek refuge, feed, and delay their passive transport for varying periods as needed to complete each developmental stage (egg, fry, smolt, adult). Strung together the physical features in each environment and at each ontogenetic stage constitute a chain of habitats in time and space that salmon navigate to complete their life cycles and maintain membership in a population.

Abundance and Variability

A second important component of the member/vagrant hypothesis is the assumption that temporal variability in abundance is determined by the loss of individuals from the area that ensures membership within a given population (Sinclair 1988). This idea suggests that loss of members from a population (vagrancy) occurs throughout a life cycle and may be the result of biological interactions or purely physical (geographic) factors. Sinclair distinguishes what he calls spatial processes, which involve geographic displacement from the area and time necessary to ensure population membership, from energetics processes, which include mortality from predation, competition, or disease. Spatial losses may result from advection of individuals away from the area/time necessary to complete their life cycle. Such losses do not necessarily require mortality of individuals but simply the failure to find a mate or reproduce successfully within the appropriate area and time.

Adult salmon vagrants (strays) include individuals that return to spawning grounds outside their natal stream. Some level of straying may be evolutionarily advantageous, allowing species to test new environments, increase genetic heterogeneity, and expand their range or recolonize habitats destroyed by disturbance. However, many strays may simply not contribute to the next generation, because they fail to find a mate at the precise time or place of return or because their genetic patterns of emergence, rearing, and migration are mismatched for the conditions represented in a new environment. Using electrophoretic analysis, for example, Tallman and Healey (1994) estimated that gene flow among chum salmon populations in Vancouver Island streams was less than 5%, although straying rates estimated from tagging studies were considerably higher (as much as 46% in one instance). These results suggested that most strays to nonnatal streams did not reproduce successfully.

Spatial and energetics losses may involve either density dependent or independent processes. However, the member/vagrant hypothesis suggests in principle that spatial processes alone can be sufficient to account for density-dependent losses from a population. The size of the geographic area capable of maintaining members of a population, for example, determines its carrying capacity and controls fish density (Sinclair 1988). This mechanism has been suggested to explain strong year-classes of sardines (*Sardinops melanostictus)* off Japan, when oceanographic changes expand the total area available for successful spawning and prey production, and increase the survival of post-larvae (Lluch-Belda et al. 1992). Climatically driven expansion or contraction of the ocean habitat area suitable for survival also might be important for salmon in the Pacific Northwest, which is located near the subarctic boundary of the North Pacific and encompasses the southern edge of the range of several salmon species (Fulton and LeBrasseur 1985, Bottom et al. 1998).

Applications of the Theory to Salmon and Estuaries

The member/vagrant hypothesis has a number of important implications for understanding the structure and dynamics of salmon populations:

- First, if the hypothesis is correct, then salmon populations and life history types should exhibit a geographic structure associated with the varied features and characteristic patterns of variability encountered across their broad distributional range.
- Second, such a complex life history structure should maximize productivity and resilience of salmon by diversifying habitat use and spreading risks unevenly in time and space.
- Third, unlike traditional population theories, the hypothesis suggests that a variety of geographic and density-independent processes throughout all stages of the salmon life cycle might explain fluctuations in population abundance.

The following evidence offers support for these conclusions and suggests that Sinclair's (1988) hypothesis can provide a general framework for evaluating the role of estuarine habitats in salmon life cycles.

Geographic Structure of Populations and Life Histories

Biologists have documented examples of the complex geographic structure of salmon populations and described considerable life history diversity within and among populations (e.g., Taylor 1990, Healey and Prince 1995) consistent with the patterns expected from Rich's (1939) observations and Sinclair's (1988) hypothesis. Yet the importance of this geographic structure to observed patterns of estuarine residency and habitat use has rarely been considered in salmon research and management. Nonetheless results from several population studies in the past few decades support the member/vagrant hypothesis and its application to salmon in estuarine environments.

Perhaps the best example is a detailed study of Chinook salmon life histories in the Sixes River in Oregon. Within this small watershed, Reimers (1973) documented five different life history types of Chinook salmon based on the patterns of seaward movement by juveniles (Table 3). By comparing migration and rearing patterns of outmigrants with those recorded on the scales of returning adult salmon, Reimers concluded that approximately 90% of the fish returning to spawn were Type 3: those that had spent an extended period of time in the late summer rearing in the estuary where they grew to a large size before migrating to the ocean. Yet this was not the most abundant pattern among the juveniles Reimers sampled.

Although Reimers' (1973) results are often cited to demonstrate that extended estuarine rearing and growth are critical for Chinook salmon, it is possible that if he had studied several broods of Chinook, he might have found other life history types that survived equally well during other years and environmental conditions. This possibility is supported by an experiment that compared the survival of Campbell River juvenile Chinook released in British Columbia over three broodyears into four different environments (Macdonald et al. 1988, Levings et al. 1989):

1) the river,
2) the estuary,
3) an offshore transition area, and
4) the ocean.

Table 3. Juvenile life history types for Chinook salmon in the Sixes River (Reimers 1973).

Life history type	Pattern of seaward movement
1	Fry move directly to sea within a few weeks
2	Juveniles stay in the river or tributaries until early summer, move to the estuary for a short period, and go to sea before late summer
3	Same as above except fish stay in the estuary through late summer and go to sea in the autumn
4	Juveniles stay in tributaries until autumn rains and then migrate to sea
5	Juveniles stay in tributaries through the summer, rear in the main river the following spring, and enter the ocean as yearlings

Although fish with access to the estuary (groups released upriver or directly in the estuary) had a higher survival to return during the first two years of the experiment, in the third year, survival was about equal for all four release groups. Thus changing environmental conditions from year to year may favor different rearing and migration behaviors within a river system.

In the Nanaimo River in British Columbia, Carl and Healey (1984) identified three juvenile life history types for Chinook salmon associated with differences in their age of seaward migration, including subyearling estuarine smolts (fry move directly to the estuary and enter the ocean in June or July), subyearling riverine smolts (fry rear in the river two months and briefly in the estuary before entering the ocean), and yearling riverine smolts (juveniles stay in the river a full year and move seaward in the spring). Genetic isolation of the three life history types was suggested by variations in allozyme frequencies and differences in body morphology of each type. Carl and Healey (1984) concluded that variations in migration behavior within the Nanaimo River basin are linked to different subpopulations associated with geographically distinct spawning areas. Thus, as suggested by the member/vagrant hypothesis, subpopulations have developed around specific geographic settings where different groups of salmon complete their life cycles through different times and ages of migration.

The present-day distribution of Chinook salmon in the Columbia Basin also reveals a geographic structure of spawning populations and juvenile life histories, although it is a fragmented remnant of the mosaic of spawning races and life history types that once existed (ISG 2000, Williams in press). Stream-type (yearling migrant) life histories today are most common in the Columbia River headwater streams and in the Snake and Salmon rivers subbasins, while ocean-type (subyearling migrant) life histories predominate in lower reaches of the Columbia (Taylor 1990).

These present-day patterns generally coincide with different adult spawning runs: ocean-type life histories today are most often associated with fall spawning runs in the lower reaches, and stream-type are common among spring and summer-run adults in the upper basin. The Independent Scientific Group (ISG 2000) found that this presumed dichotomy of juvenile migrant types based on adult run timing is an oversimplification that ignores upriver habitat losses and associated ocean-type life histories that were likely prevalent among some spring and summer spawning populations. Nonetheless the general principle of a geographic structure of life histories associated with particular habitat features applies to salmon populations in the Columbia River basin.

Salmon Resilience and Production

The geographic structure of salmon populations and the diversity of life histories within and among populations have been described as a strategy that spreads risks and avoids brood failure (Healey 1991). Because not all individuals behave in the same manner or use the same habitats at the same time, life history diversity affords resilience to salmon in uncertain environments. The use of different spawning and rearing areas maximizes the possibility that any year-class will contribute to future generations and maximizes the total production of juveniles from a river system (Carl and Healey 1984).

The importance of life history diversity is illustrated by the effects of various ocean disturbances on populations that leave estuaries at different times or rear in different areas. Although the population-specific patterns of ocean migration are poorly understood, gross differences among geographically distinct groups of populations (stocks) may affect the capacity of salmon to withstand strong El Niño events or interdecadal shifts in ocean regimes (e.g., Mantua et al. 1997). Tule fall Chinook stocks, which spawn in the lower Columbia-Bonneville pool area, migrate primarily off Washington and southern British Columbia, whereas upriver brights[3] from the area between the McNary and Priest Rapids dams rear far north off northern British Columbia and southeastern Alaska (Van Hyning 1973, Beaty 1992). Coastal Chinook stocks south of Cape Blanco in Oregon rear off southern Oregon and northern California, while stocks to the north of Cape Blanco migrate northward (Nicholas and Hankin 1988).

Differences in ocean rearing areas may explain different responses to the strong 1982–1983 El Niño event: Chinook stocks off southern Oregon and locally distributed stocks from the lower Columbia River suffered high mortality and low returns, whereas northward migrating populations from the Columbia River showed little or no decline in abundance (Johnson 1988).

Differences in the timing of migration of salmon from the estuary to the ocean also may affect the capacity of salmon to adapt to variable ocean conditions. While coho salmon production, for example, has been positively associated with periods of strong coastal upwelling in the spring (Nickelson 1986), the timing, strength, and duration of upwelling events is episodic and variable along the coast. The seasonal shift from winter conditions to a spring/summer upwelling regime, characterized by changes in winds, coastal currents, temperatures, and density gradients, occurs suddenly at different times each year (Huyer 1983, Strub et al. 1987).

A single upwelling event lasting a few days in the spring may be sufficient to cause the shift to a spring/summer regime (Huyer 1983). Thus different times of ocean migration may be advantageous in different years depending, for example, on the onset of the spring/summer transition, the timing and location of upwelling events, the distribution of the Columbia River

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[3] Bright is the common name for a particular run of Chinook salmon in the Columbia River basin.

plume, or the northward extent of warming caused by occasional strong El Niño Southern Oscillation (ENSO) events in the tropics (ISG 2000, Williams in press).

Spence (1995) concluded that variability in ocean entrance by coho salmon has evolved in response to characteristic degrees of ocean variability in different regions of the North Pacific. Comparing 50 smolt populations from California to Kodiak Island, Alaska, Spence described latitudinal patterns in the timing, duration, and variability of migration. Although migration times varied locally, results suggested that this variability exists within certain temporal windows of opportunity among different regions of the North Pacific. Spence further concluded that a more protracted period of migration among coho salmon populations south of the Queen Charlotte Islands in British Columbia is possibly an adaptive response to increased ocean variability and uncertainty relative to more northern areas.

Diversity of salmon life histories not only minimizes risk in uncertain environments, it is fundamental to salmon productivity. As conditions in freshwater, estuarine, and marine environments vary between years, so may the number of alternative behaviors that will permit life cycle closure. In relatively favorable conditions a greater number of life history types and populations may be captured, producing a stronger year-class for the species as a whole (Figure 8, [Bottom et al. 1998]). Thus as proposed by the member/vagrant hypothesis (Sinclair 1988), the absolute abundance of a species may be a function of physically driven expansion and contraction of the spatial (and temporal) extent of areas where life cycle closure is possible.

Life history diversity thus may affect the overall carrying capacity of an estuary for salmon. Some studies present evidence of density-dependent estuarine growth of salmon, which could affect size at ocean entrance and, through size-specific mortality, ocean survival of smolts (Reimers 1973, Reimers et al. 1979, Healey 1982, Nicholas and Downey 1983, Nicholas and Hankin 1988). As illustrated by the varied life history types in the Sixes (Reimers 1973) and Nanaimo rivers (Carl and Healey 1984), density-dependent effects may be minimized if the contributing populations of each species in a basin have somewhat different times and sizes at entrance, duration of residence, and migratory paths through the estuary. By spreading their rearing patterns through time and space, not all salmon use the same areas and resources at the same time. Variation in life history thus maximizes basin productivity by allowing a continued turnover of available estuarine habitat by different groups of fish staged to move through the system at different times (Myers and Horton 1982).

Salmon Imprinting and Homing

Added support for the member/vagrant hypothesis comes from studies of salmon imprinting and homing. These results suggest that the idea of salmon navigating a chain of habitats to complete their life cycles may be literally (and not just metaphorically) correct. One hypothesis of the mechanism of homing suggests that juvenile salmon imprint on a series of olfactory signatures as they migrate through a gradient of habitats to the ocean and retrace this sequence upon returning to their home streams (Harden Jones 1968, Dittman et al. 1996). In experiments to test imprinting of coho salmon at various life stages, Dittman et al. (1996) concluded that simple exposure to odors may not be sufficient but that olfactory stimuli experienced by migrating through a gradient of environmental cues—varying water chemistry, temperatures, lunar cycles, and water velocities, etc.—may be necessary for optimal imprinting.

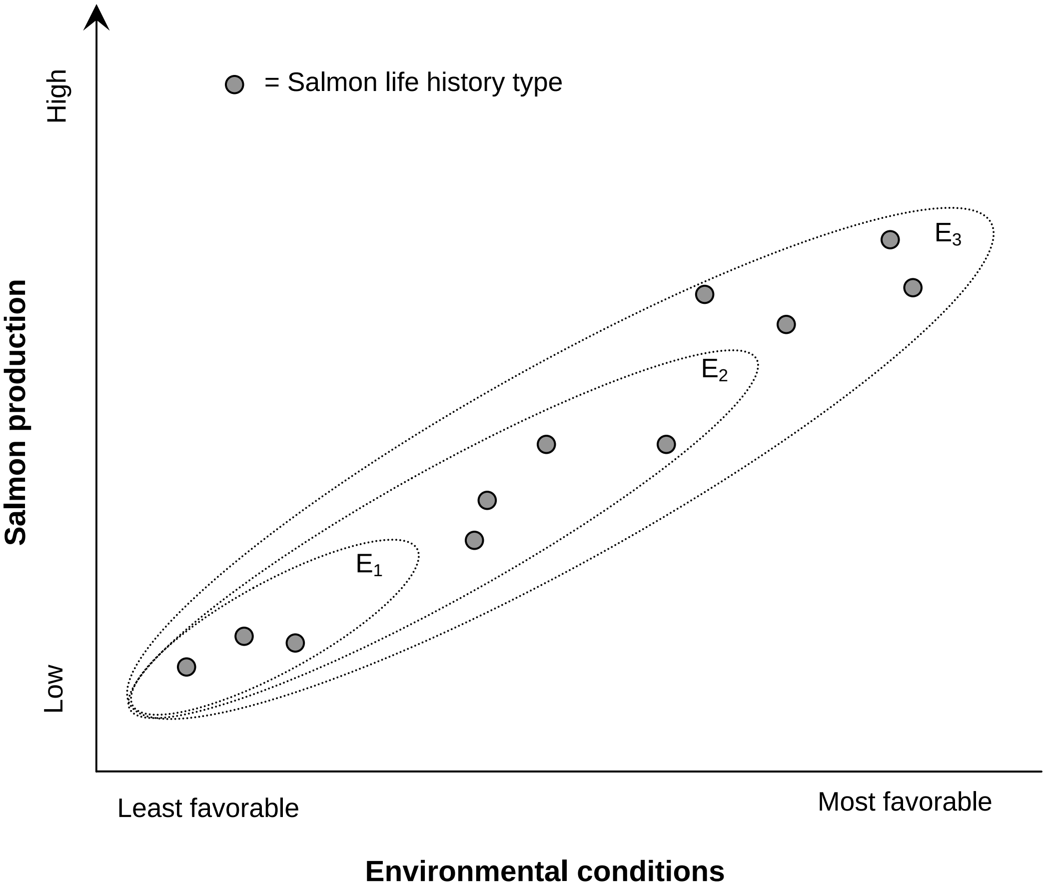


Figure 8. Salmon production as influenced by life history diversity. Each life history type experiences a different environment based on the temporal and spatial sequence of habitats (freshwater, estuary, and ocean) used throughout its life cycle. As conditions (e.g., E_1, E_2, and E_3) become more favorable, the ecosystem captures (i.e., expresses) a greater variety of life histories, producing a stronger year-class for the species.

A proposed mechanism for this response to migration is the apparent stimulation of thyroxine production by varying environmental cues, which may facilitate olfactory imprinting (Dittman et al. 1996).

A highly sensitive period for imprinting is the end of the parr-smolt transformation. Dittmann et al. (1996) found little evidence that hatchery salmon imprinted to homing cues before the smolt stage. Fish held for lengthy periods and not allowed to migrate during the parr-smolt transformation were impaired in their homing ability. This suggests that conditions experienced during migration through the tidal-freshwater and estuarine gradient, where salmon gradually adapt to saltwater conditions and reach the end of the smolt stage, may be particularly important to successful imprinting. Interestingly, although wild fish show a capacity to imprint at early ages before the smolt stage, hatchery presmolts in these experiments did not. A stable environment and lack of migration associated with hatchery rearing may have been the cause of this (Dittman et al. 1996).

Geographic Mechanisms of Population Control

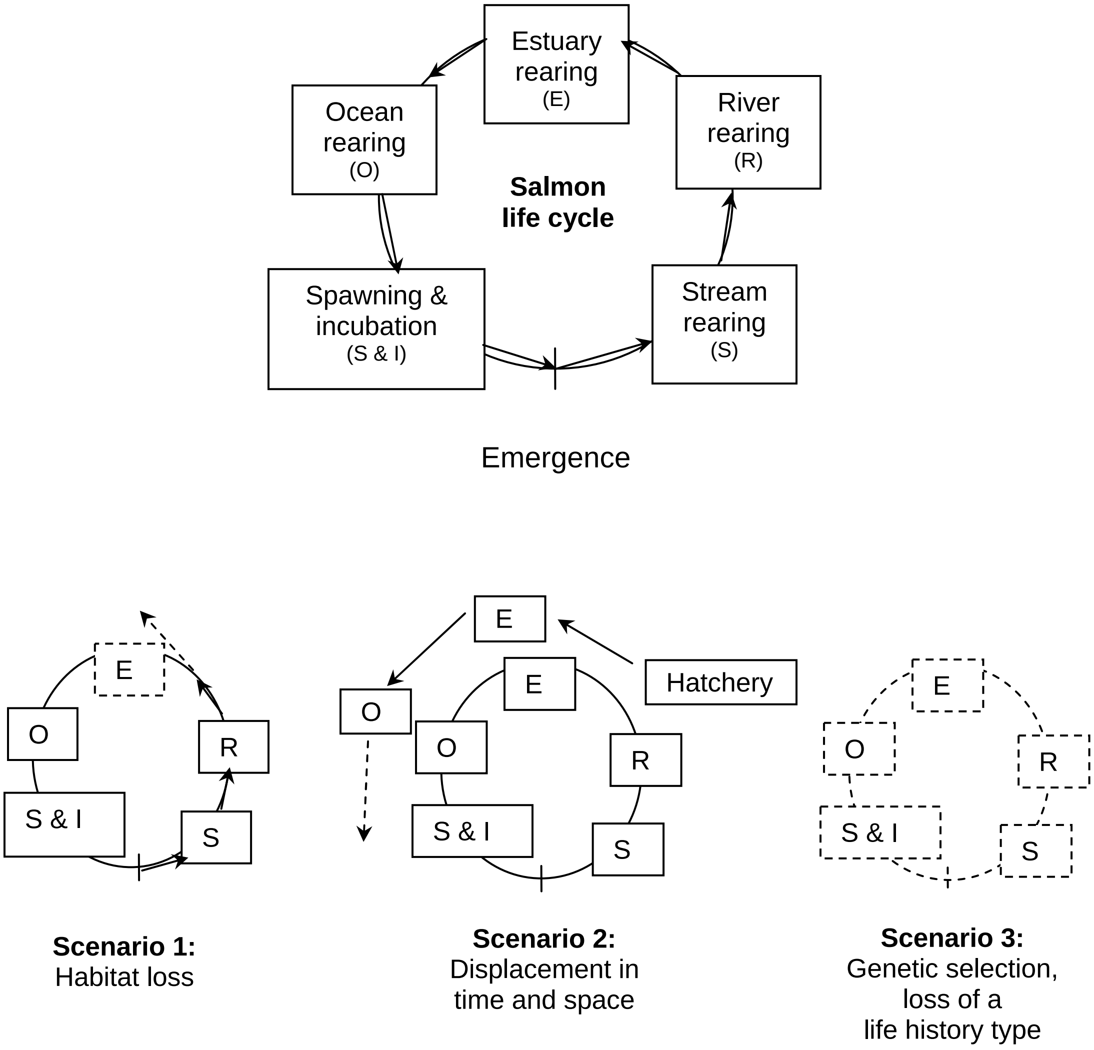
In addition to mortalities associated with competition, predation, and disease, the member/vagrant hypothesis underscores the importance of geographic processes of population control for species that migrate among spatially distant habitats. Even biological interactions at a local scale may be controlled by physical processes that determine, for example, the temporal and spatial availability of salmon habitat or the particular suite of species that salmon encounter when they enter the ocean. Patterns of salmon abundance and use in an estuary also are linked directly to various processes upriver that determine the size, migration timing, and physiological state of downstream migrants. Mechanisms of population control implied by the member/vagrant hypothesis (Sinclair 1998) that may be particularly relevant for understanding salmon in estuaries are described in the following subsections and depicted in Figure 9.

Habitat availability and connectivity

If salmon migration and rearing behaviors are tied to specific geographic features, then population members may be lost if these features are changed or eliminated by natural or human causes (Figure 9, Scenario 1). Scale analyses comparing past and contemporary life histories among Rogue River Chinook salmon in Oregon, for example, suggest that a former estuarine-rearing life history may have been eliminated, possibly through modifications of the tiny estuary during construction of the jetties and boat basin (Schlucter and Lichatowich 1976). A review of the five life history types described in Sixes River (Reimers 1973) raised similar questions about whether warming of the mainstem river possibly eliminated an early large migrant pattern, which is found in other coastal estuaries (Bottom et al. 1998). Extensive loss of historic estuarine wetlands through widespread diking and filling in Northwest estuaries could reduce or eliminate some subyearling migrant life histories that have been linked to the availability of shallow marsh habitats (e.g., Levy and Northcote 1981 and 1982).

If salmon life cycles require specific sequences of habitat in time and space, then areas otherwise capable of supporting salmon may remain unoccupied when their connection to other habitats is lost (Bottom et al. 1998). Thus habitat conditions and associated subpopulations upriver may ultimately limit the array of life histories expressed in the estuary. Certain estuarine habitats might not be fully occupied, for example, if upstream habitats lost to dam construction, pollution, or other factors supported populations with distinct estuarine rearing behaviors.

One example noted above is the loss of some ocean-type life histories among Chinook salmon populations in the Columbia River (ISG 2000, Williams in press). Temperature variations affecting growth opportunity and time of smolting in different areas of the basin may be an important factor determining the geography of Chinook life histories (Taylor 1990). Dam construction combined with temperature increases in the main stem and lower subbasins have diminished habitat opportunity upriver and substantially reduced the proportion of subyearling (ocean-type) migrants that are now produced in the Columbia (ISG 2000, Williams in press). Loss of subyearling migrant types from summer and spring spawners probably has occurred in many areas that historically offered optimal growth opportunity, particularly the warmer middle portions of the Columbia River subbasins (Lichatowich and Mobrand 1995, ISG 2000, Williams in press). Because subyearling migrants typically reside in the estuary for longer periods and use different habitats than those with yearling life histories, such losses could have an important



Scenario 1: Habitat loss

Scenario 2: Displacement in time and space

Scenario 3: Genetic selection, loss of a life history type

Figure 9. Generalized view of a salmon life cycle (top) and three scenarios of spatial losses that can affect life cycle closure (bottom). In Scenario 1, habitat losses in the estuary prevent extended periods of estuarine rearing and growth prior to ocean entry (dotted arrow and estuary-rearing box indicate loss after the river-rearing stage). In Scenario 2, hatchery rearing modifies the migration sequence—timing, distribution, and developmental stage—which may prevent optimal imprinting and homing back to a river basin (external hatchery pathway without a connection to the spawning stage). In Scenario 3, intensive selection pressures (e.g., harvest, interbreeding with hatchery fish, etc.) modify the genetic composition of a population, eliminating particular life history pathways that are genetically programmed (dotted lines and absence of arrows).

influence on contemporary patterns of estuarine rearing by Chinook salmon and could leave vacant various shallow-water habitats favored by smaller ocean-type juveniles.

Disturbance processes

Changes in disturbance processes that displace salmon from the appropriate time and location needed to complete their life cycles or that reduce availability of critical habitats may contribute to population losses. It is probable that Columbia River salmon diversified their migration and rearing behaviors to fully use the wide array of tributary habitats and flow conditions historically represented in the Columbia River basin. Because populations varied widely in their migration timing and behaviors, Columbia River salmon were not equally vulnerable to environmental disturbance. Disturbance conditions most favorable for one life history type may have been detrimental to another. However, if the relative benefits of various behaviors changed from year to year, the diversity of life histories would be maintained (ISG 2000, Williams in press).

Regulation of flows in the Columbia River by mainstem dams has dampened natural fluctuations in the system and may have created a mismatch between certain migration behaviors and the flow/habitat conditions that now exist. Stabilization of river flows and establishment of a system of slack-water reservoirs, for example, possibly shifted the fitness landscape toward less-favorable conditions for salmon with subyearling life histories, whose migration and feeding behaviors depend on flooded shorelines and complex backwater areas maintained by the interaction of the river with riparian and floodplain habitats (ISG 2000, Williams in press). Flow regulation may similarly influence access to habitats in the estuary because of changes in salinity structure, water velocity, and depths.

Displacement of fish in time and space

Artificial manipulations of salmon development (e.g., smolting), release locations, and migration timing may contribute to population losses by altering the time and space use of estuarine and marine habitats and increasing rates of straying by adults (Figure 9, Scenario 2). The large proportion of hatchery Chinook salmon now released in the Columbia Basin (see the “Estuarine Development History and Salmon Decline” section, page 5), many of which are held for extended periods and raised to relatively large sizes, could substantially affect size and time-dependent rearing and migration patterns in the estuary.

In studies on the effects of release date and transportation on hatchery Chinook salmon from two Columbia River hatcheries, Pascual and Quinn (1995) documented varying effects on homing ability, which they attributed to disruptions in the sequence and timing of imprinting events through artificial manipulations. From these and other studies, they suggest that the sequence of imprinting events is characterized by the time fish experience a particular location and the physiological state of the fish at that time. Thus manipulations of release date and transportation of fish may disrupt the migration sequence and increase straying through effects of release date on spawning time, effects of holding fish on the sequence of juvenile imprinting, and interference of imprinting through off-station transport of smolts (Table 4).

Population losses due to disruption of the migration sequence are illustrated by the experiments of Solazzi et al. (1991) who compared the survival of hatchery coho salmon released directly into the estuary and various distances offshore. The results showed progressively greater rates of straying to river basins outside the Columbia River with transport distance from the hatchery rearing site. The level of homing reported for some Columbia River hatcheries is much lower than has usually been reported for salmonids, indicating significant spatial losses and raising concerns about genetic interchange among populations (Quinn et al. 1991).

Table 4. Possible mechanisms of increased straying of fish through hatchery and transportation manipulations (from Pascual and Quinn 1995).

I. Effects of release date
  A. Affects time of return
    1. Month at return
    2. Age at return
  B. Affects sequence of imprinting by seaward migrating fish
    1. Mismatch between the location and developmental state of fish
    2. Mismatch between the location and the time (e.g., environmental conditions)

II. Effects of transportation
  A. Reduced opportunity to imprint
  B. Genetic adaptation to local conditions

Population structure and life history

Many life history variations in salmon populations have been demonstrated experimentally to be under some degree of genetic control, including age at maturity (Hankin et al. 1993), time of spawning and rate of egg and larval development (Beacham and Murray 1987), growth rate of juveniles, and age of seaward migration (Carl and Healey 1984, Taylor 1990). Strong selection pressures through harvest, hatchery practices, or other factors that alter the genetic structure of Columbia River populations may thus affect the patterns of migration and rearing through the estuary even if the habitats needed to support each life history type are available (Figure 9, Scenario 3).

Changes in the time salmon spawn (and therefore emerge) may be critical to match subsequent developmental stages and life histories to various time windows in the environment (e.g., Beaty 1992, Spence 1995). Einum and Fleming (2000), for example, demonstrated a causal link between time of breeding (and thus time of hatching and emergence) and the success of offspring in Atlantic salmon. In this case, later emerging juveniles were smaller than early emerging ones so that reproductive success also could be affected through differential size selection at subsequent life stages.

In the Salmon River in Oregon, the spawning time of coho salmon has advanced 1–2 months, and the duration of spawning activity has decreased since the hatchery began operating in the mid-1970s (Mullen 1978, 1979, Jacobs unpubl. data). Although the specific effects on juvenile rearing patterns in the estuary are uncertain, such changes undoubtedly influence the times of emergence and downstream migration. In recent years, early adult returns has meant that few if any coho salmon spawned after late November flood events, which likely reduced survival of eggs already in the gravel. The possibility of a mismatch between present spawning times and the Salmon River environment is suggested by the lack of successful recruitment from most naturally spawning hatchery fish: each year about 95% of the fish spawning naturally in Salmon River are adults produced from a new hatchery brood (Jacobs et al. 2000).

A Framework for Evaluating Estuarine Requirements of Columbia River Salmon

Evaluation Principles

To summarize, the member/vagrant hypothesis (Sinclair 1988) and the supporting evidence from studies of salmon populations and life histories offer the following principles as an alternative to production thinking (Table 1) for interpreting the role of estuaries in salmon life cycles:

- Salmon have evolved complex life cycles that require a chain of habitats in spatially discrete environments (freshwater, estuary, and ocean).
- The resilience and productivity of salmon species depend on their diversity of life histories, including variations in the use of estuarine habitats by juveniles.
- The geographic pattern and diversity of salmon life histories reflect the variety of habitat combinations in time and space by which each species can complete its life cycle.
- Estuaries offer one of many alternative rearing opportunities for salmon to achieve life cycle closure. Salmon with subyearling life histories are among the most dependent on estuaries for juvenile rearing.
- Variability in salmon abundance is a result of losses from the time/area necessary to ensure membership in a population. Such losses may occur throughout all stages of the salmon life cycle and may involve geographic (spatial) and biological (energetics) processes that may be density-dependent or independent.

These principles emphasize the interaction between behavior (life histories) and various habitat features that salmon use to complete each stage of their life cycle and maintain membership in a population. Thus conservation of population richness requires protection of the diverse geographic features that salmon use to achieve life cycle closure (Sinclair 1988).

From an evolutionary perspective, Healey and Prince (1995) similarly describe the diversity of salmon rearing behaviors as the consequence of unique salmon genotypes interacting with available habitat features. Thus different combinations of habitat and genotype result in a variety of phenotypic behaviors by which salmon can successfully complete their development and reproduce. Among these behaviors are varied times and ages of salmon migration, periods of residency in the estuary, and times and sizes of ocean entry, all behaviors that require a particular temporal and spatial sequence of habitats to support them.

The total productive capacity of the Columbia River basin and the resilience of salmon species are a function of all combinations of genotype and habitat that allow for the full expression of salmon rearing and migration behaviors, including diverse life histories in the estuary. To maintain the diversity and productivity of salmon requires the conservation of populations within their habitats, protecting the full variety of genotype-phenotype combinations (Healey and Prince 1995).

Evaluation Criteria

It follows logically from the "Evaluation Principles" subsection that the productive capacity of the Columbia River estuary can be affected by any changes that sever the link between salmon behavior and habitat, including the various categories of spatial losses depicted in the examples in Figure 9:

1) removing habitats, altering habitat functions, or changing disturbance processes that salmon require to express the full diversity of potential rearing behaviors,
2) altering the geographic structure and genetic characteristics of the component populations of each species that converge in the estuary en route to the ocean, and
3) changing the phenotypic behavior of salmon, including displacement of fish from the time/space sequence of habitats they need to complete their life cycles in their home streams, regardless if the underlying genetic structure of populations is affected.

In consideration of these and other categories of change implied by the member/vagrant hypothesis (Sinclair 1998), including the role of energetics losses from populations, we patterned our evaluation of estuarine-rearing conditions on the following criteria (Figure 10):

- Habitat opportunity—the availability of estuarine habitat for salmon, often determined by physical (spatial) processes.
- Habitat capacity—the quality of estuarine habitat for salmon, determined by biological interactions and bioenergetic conditions (energetics processes).
- Population structure/life history—phenotypic and genotypic effects at other life stages that are linked to salmon behaviors in the estuary.
- Performance—the ultimate outcome for salmon within the estuary, as measured by growth, life history diversity, and foraging success.

We discuss our definition of each criterion and its application in the following subsections.

Habitat opportunity

Opportunity involves the capability of juvenile salmon to access and benefit from occupying a habitat. We define this capability broadly based on physical factors, physiological constraints, and ecological interactions (Sanfriel and Ben-Eliahu 1991, Simenstad et al. 2000b). These factors involve spatial processes that are largely unaffected by fish density (Table 5).

We distinguish opportunity to occupy habitat from the probability of doing so. Probability involves many other external factors that affect whether juvenile salmon access habitat (i.e., variability in salmon populations and life histories that dictate run timing and fish size, density-dependent interactions, the presence and practices of salmon hatcheries, etc.) Thus whether a habitat is occupied at a particular time does not affect opportunity.

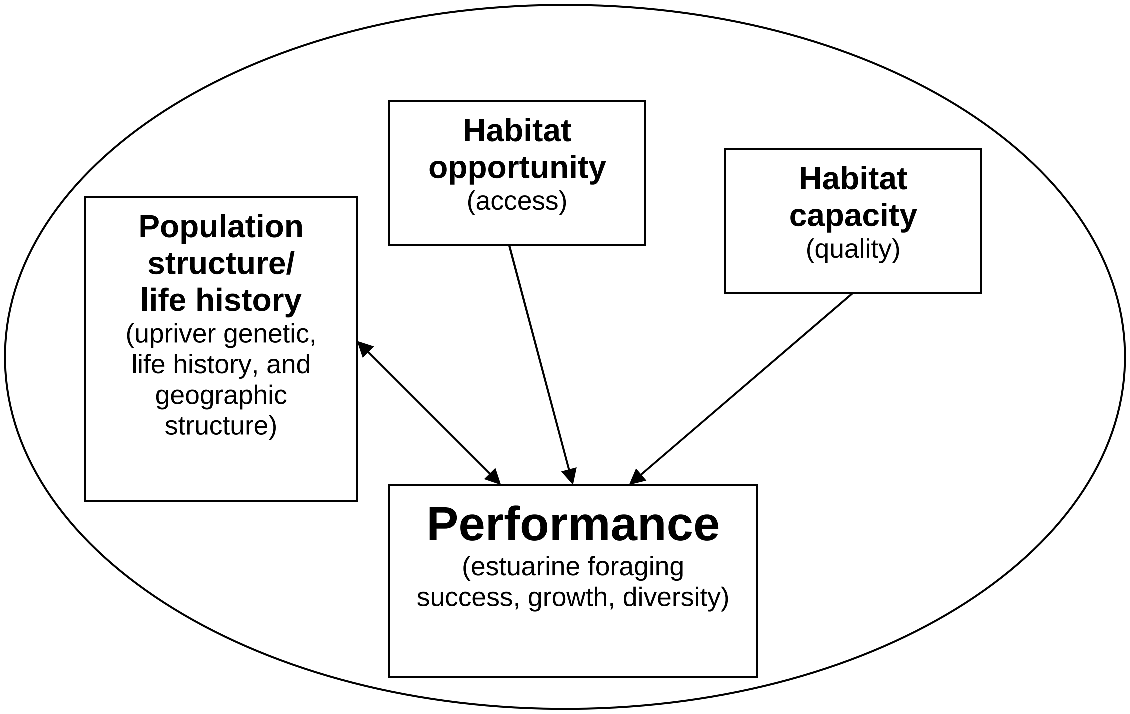


Figure 10. Criteria for evaluating estuarine-rearing conditions for subyearling ("ocean-type") salmon as implied by the member/vagrant hypothesis (Sinclair 1988).

Table 5. Factors affecting estuarine-habitat opportunity for juvenile salmon.

Physical	**Physiological/ behavioral**	**Water characteristics and quality**	**Ecological**
Tidal flooding Depth Duration Fluvial flooding Frequency Depth Duration Timing Distributary and tidal channel structure	Water velocity Turbidity	Temperature Salinity Dissolved oxygen Turbidity Toxicants	Proximity to disturbance (e.g., noise, movement, etc.) Refugia from predation (e.g., extent of overhanging vegetation, marsh vegetation height, proximity to deepwater habitats)

We first describe historical patterns of environmental disturbance, specifically climate and river flow, which regulate the physical state of the basin-wide ecosystem within which the estuary is embedded. Climatic and hydrologic processes set broad limits in estuarine habitat opportunity while exerting direct selection pressures on salmon populations. In the "Changes in Hydrological Conditions" section (page 47), we examine natural climatic variations and human-induced changes in river flow and sediment transport that could have an overriding influence on estuarine-habitat opportunities and capacities for Columbia River salmon.

Following this basin-wide assessment, we apply a hydrodynamic modeling approach to evaluate the sensitivity of salmon-habitat opportunity to historic changes in river flow as well as bathymetric conditions within the estuary in the "Estuarine Habitat Opportunity" section (page 89). The purpose is to determine whether modeling is a useful tool for predicting habitat-opportunity change and the potential salmonid response to past and future management scenarios. For these analyses, we use depth and velocity as indicators of habitat opportunity for subyearling Chinook salmon in the "Subyearling Chinook Salmon as an Indicator of Estuarine Conditions" subsection (page 44). We chose these criteria because:

1) they are important physical features to which juvenile salmon respond,
2) they can be simulated with some accuracy by modeling (as compared to water characteristics or quality), and
3) they are useful descriptors of the major physical changes that have affected conditions in the estuary.

Habitat capacity

We define capacity to support juvenile salmon as those habitat qualities that promote juvenile-salmon production, including conditions necessary for feeding, growth, growth efficiency, and eluding predators (see the "Estuarine Habitat Capacity" section, page 127). Capacity thus encompasses what Sinclair (1988) terms energetics processes, including biological interactions and bioenergetic relationships:

- productivity of selected invertebrate prey, including quantity and availability,
- physicochemical and ecological conditions that maintain prey production,
- salinities and temperatures that promote high assimilation efficiencies, and
- predation levels as affected by habitat structure and relative vulnerability of salmon (e.g., refugia in vegetation or shallow water) as well as the habitat attributes of predators.

Capacity is time dependent, because prey production can be punctuated, and predation intensity may vary with alternative prey availability, food demands, etc. Many variables interact to affect capacity. Turbidity may reduce the feeding efficiency and growth potential of salmon in a particular habitat and, at the same time, reduce their vulnerability to predators. In contrast to the physical factors that regulate habitat opportunity, the variables affecting habitat capacity are often density dependent. Salmon abundance may affect food-consumption rates and predation levels.

Life history/population structure

Whether salmon fully realize the opportunity and capacity of the estuarine habitats available to them may depend heavily on factors at other life stages that affect fish behaviors and their patterns of estuarine use. Such effects may be entirely phenotypic (e.g., changes in fish size and times of migration associated with hatchery release schedules, transportation of fish around dams, or changing temperatures or flow regimes); however, selection pressures from hatcheries, harvest, or elimination of upriver habitat also may alter the underlying genetic and geographic structure of upriver populations and thereby eliminate certain rearing behaviors. Changing release dates from hatcheries, for example, may alter time and age of return, with subsequent effects on emergence times and downstream patterns of estuarine use. Loss or substantial decline of upriver populations through overharvest of wild stocks or loss of spawning habitats may eliminate various combinations of genotype-habitat interaction that are responsible for unique life history patterns downstream. Although the focus of this study is the estuary, our conceptual approach dictates that we also must be aware of genetic or behavioral factors at other life stages that can influence the juvenile-salmon estuarine performance. Similarly, performance within the estuary may affect salmon population structure and associated marine and freshwater life histories (Figure 10).

Performance

The ultimate measure of performance for Columbia Basin salmonids is the diversity of self-sustaining populations within their natal habitats, which is reflected in the overall resilience and productivity of each species from the basin as a whole. For the purpose of this evaluation, performance is defined more narrowly based on the diversity of physiological and behavioral patterns of subyearling Chinook within the estuary. We assume that the diversity of habitat-specific residence times, range in migration timing, growth, and foraging success in the estuary are all indicators of the relative capacity of the estuary to accommodate Chinook salmon and all the component populations and life history types. In the "Change in Juvenile Salmon Life History, Growth, and Estuarine Residence" section (page 142), we compare historic and present life history diversity of juvenile Chinook salmon in the Columbia River estuary.

Our conceptual approach suggests that optimal performance in the estuary as defined by these indicators also will favor salmon diversity and productivity in the basin as a whole. We interpret salmonid performance and the effects of flow regulation in light of our results for all three factors:

1) opportunity,
2) capacity, and
3) life history/population structure.

Subyearling Chinook Salmon as an Indicator of Estuarine Conditions

The patterns of habitat use within the Columbia River estuary vary among salmon species and life history types within species (Figure 11). Juvenile pink salmon, sockeye salmon, or steelhead likely spend the least amount of time in the estuary. Various life history types of

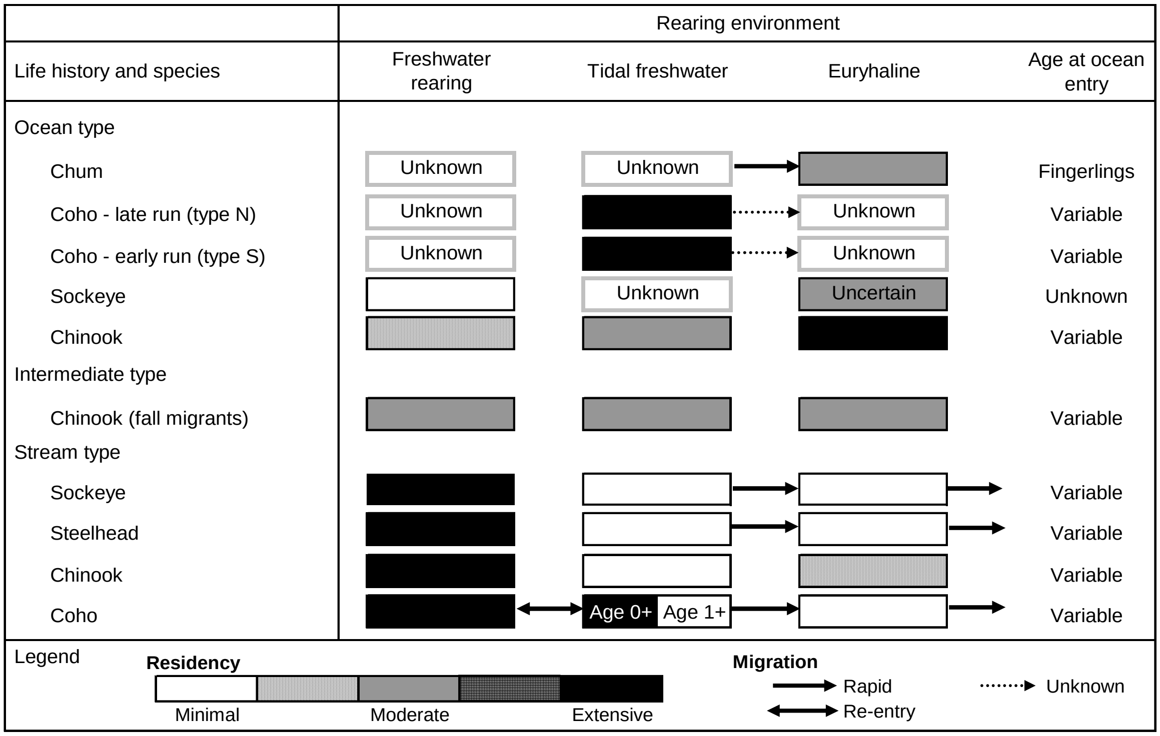


Figure 11. Proposed model of relative migration rates and residence times for salmonid species in freshwater and estuarine rearing environments of the Columbia River basin.

Chinook and most chum salmon may remain for longer periods, while they actively feed and grow before ocean entrance (Healey 1982, Thorpe 1994). Although coho salmon may use estuarine habitats for significant periods, particularly in the tidal-freshwater zone (and there is increasing evidence that subyearling migrants in some estuaries may grow rapidly enough to migrate to sea in their first year of life), we have insufficient data to verify estuarine life histories of coho in the Columbia River.

Two major types of life history are commonly distinguished among Chinook salmon:

1) stream-type juveniles that rear in freshwater for at least a year before migrating directly to sea, and
2) ocean-type juveniles that spend variable amounts of time in the river and estuary before migrating seaward as subyearlings.

For this evaluation, we emphasize subyearling Chinook salmon, because they have the longest period of estuarine residency among salmonids, and past surveys provide at least some information to interpret variations in their rearing behavior. Results for Chinook also may apply to other species with subyearling migrants, particularly chum salmon.

The continuous influx of individuals to the estuary from diverse tributaries noted by Rich (1920) raises the possibility that subyearling Chinook salmon may exhibit a broader continuum of estuarine rearing and migratory tactics in the Columbia Basin than has been presumed from relatively few estuarine studies. Evaluating 11 tributaries within the lower Columbia River, Reimers and Loeffel (1967) found that juveniles from various streams either migrated immediately after emergence or remained in freshwater for as long as five months. Rich (1920) found that some individuals enter the estuary soon after emergence where they may remain for up to several months before migrating to the ocean, a pattern that has been observed in some small estuaries (Reimers 1973, Carl and Healey 1984). Duration of freshwater residence among populations scattered widely throughout the Columbia River basin may be affected by the migration distance downstream. As part of our analysis in the "Change in Juvenile Salmon Life History, Growth and Estuarine Residence" section (page 142), we reassess diversity of subyearling rearing behaviors from the results of previous salmon inventories in the Columbia River estuary.

Changes in Hydrological Conditions

Introduction

The member/vagrant hypothesis (Sinclair 1998) emphasizes the importance of certain persistent (i.e., predictable) physical features of aquatic environments around which salmonid life histories possibly developed. In the "Estuarine Development History and Salmon Decline" section (page 5), for example, we reviewed evidence that the estuarine rearing behaviors of small subyearling salmon may be adapted to productive, shallow-water habitats that are intermittently accessible during particular tide and river stages (Kukulka and Jay 2003a and 2000b). Some downstream-migrating salmon move into and out of intertidal and floodplain habitats on daily and seasonal ebb and flood cycles (Levy and Northcote 1982; Levings et al. 1986), effectively delaying their seaward transport for extended periods of estuarine rearing and growth.

The estuarine features to which salmon life histories have adapted are largely the result of riverine and tidal processes that transport sediments, other materials, and biota; establish salinity and temperature gradients; and regulate water levels and velocities. The highly productive nature of pulsed estuarine systems is a direct result of this dynamic interplay between river and tide. These interactions are not controlled entirely within the estuary, but they are determined by regional and basin-wide variations in climate, hydrology, and ocean conditions. Because these external factors establish the physical template for the entire estuary, they also directly or indirectly affect each of the major attributes of salmonid performance implied by the member/vagrant hypothesis (see the "Conceptual Framework for Evaluating Estuarine Habitat Conditions" section, page 21):

- availability of estuarine habitat (habitat opportunity),
- the quality of estuarine habitat (habitat capacity), and
- salmon population structure and life history (Figure 12).

In the "Changes in Hydrological Conditions" section, we analyze the history of basin-wide hydrologic changes and disturbances—natural and anthropogenic—that have established the physical template of the Columbia River estuary during the past 140 years. We describe the general hydrological characteristics of the Columbia River system, the data sources used in our analysis, and the regional climatic cycles and properties of subbasin flows that influence Columbia River hydrology. We analyze human and climatic effects on specific hydrological processes that are potentially important to salmonids. These processes include:

- magnitude and timing of river flow,
- fine and coarse sediment input,
- frequency of extreme events and overbank flow,
- occurrence of freshet styles, and

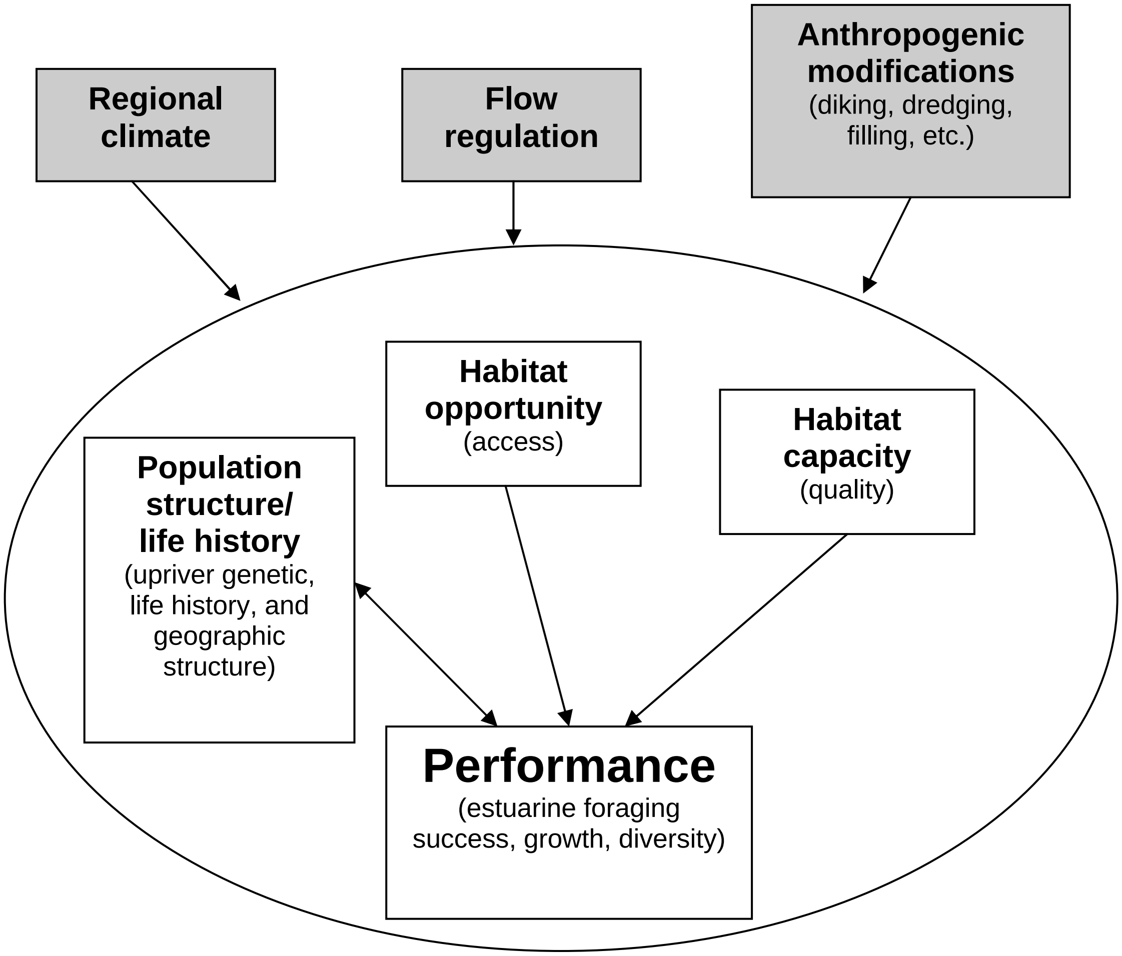


Figure 12. External factors at regional and basin scales that affect the physical template of the estuary and the performance of subyearling ("ocean-type") salmon.

- changes in subbasin flow characteristics.

We also review the implications of these results for juvenile salmon and the member/vagrant hypothesis.

General Hydrological Characteristics

The Columbia River has the largest average flow (≈7,300 m^3s^{-1}) of any river on the Pacific coast of North America; however, its sediment flow (≈10^7 metric tons per year [mt $year^{-1}$]) is less than that of the Eel River in California and that of the Fraser River in British Columbia (Church and McLean 1992, Jay and Naik 2002). The Columbia River contributes some 60% (winter) to 90% (summer) of the total freshwater input between San Francisco and the Strait of Juan de Fuca, and it strongly affects regional seawater properties of the northeast Pacific Ocean (Barnes et al. 1972).

The Cascade Mountain range divides the Columbia River drainage basin into eastern and western subbasins in Oregon and Washington. The moist and relatively warm western subbasin contains only about 8% of the total surface area of the 660,500 km^2 basin, but it contributes almost 25% of the total river flow (Orem 1968). Most of the western subbasin elevation is too low to accumulate a large seasonal snowpack. Thus the highest flows are observed during and following winter storms between December and March. Most of the eastern subbasin flow is from the seasonal snowpack melting between April and June. Much of the eastern subbasin is relatively arid, but its Canadian component experiences heavy winter snowfall and plays a major role in spring-freshet flows.

Irrigation-water withdrawal and the construction of 28 large and numerous small dams have altered Columbia River flows and sediment loads (Simenstad et al. 1992). Water withdrawal was minimal before 1890, but it increased rapidly between 1890 and 1920, and again after 1960. Dams were constructed to generate power, control floods, and facilitate irrigation. The first two dams with more than 10^6 m^3 of active storage were built on the Snake River (Jackson Lake in Wyoming, 1916, and American Falls in Idaho, 1926). The first major mainstem dams completed were Bonneville (1937, with only a modest storage capacity) on the Washington-Oregon border and Grand Coulee in Washington (1938). Seven large dams high in the basin completed between 1967 and 1973 more than doubled the storage capacity of the total dam system to 70×10^6 m^3 and provided an increase in water retention time.

These factors, plus an integrated system-management approach, suggest the 1969–1970 period as the boundary dividing the developmental (1901–1969) and modern (1970–present) periods of hydrological system management, a division we employed in data analyses. Our analyses suggested that the 19th century also had distinctive climate patterns; moreover, flow regulation was insignificant and diversions were small until the 1890s (Simons 1953). Thus the pre-1900 period (predevelopment) also is distinct (Naik and Jay 2004).

The hydrological characteristics of the Columbia River reflect regional climatic patterns. At a continental scale, base river flow decreases north to south because of glacial melt and annual snow cover. Because more northerly rivers have a stable base flow, seasonal flow fluctuations and interannual variability increase southward from the Fraser River to the Columbia eastern subbasin, to the Willamette River in Oregon, and to California rivers such as the Sacramento and San Joaquin (Milliman 1980, Berg et al. 1991, Cayan et al. 1993).

Flow regulation and water withdrawals also increase from north to south. Approximately only 3% of the Fraser River flow has been diverted compared to about 50% of the flow from tributaries to San Francisco Bay (McLean and Church 1986, Rozengurt et al. 1987). The Columbia River occupies an intermediate position with a 15–17% total reduction in flow from human and climatic factors. Furthermore, sediment transport in the Columbia River is more strongly dependent on flow than is the case in other major West Coast rivers (Jay and Naik 2002). Consequently the sediment transport regime of the Columbia River is sensitive to changes in the annual flow cycle.

Data Sources Used for Hydrological Analyses

The Columbia River daily flow record compiled by the U.S. Geological Survey (USGS 1999a) at The Dalles, Oregon, (1878–present) is the longest for any Pacific coast river. Annual maximum flow is available from 1858 (Henshaw and Dean 1915), but the dates of the maximum flows were not noted until the daily record was initiated in 1878. USGS (1999a) daily river-flow records for the Willamette River at Albany, Oregon, also were initiated in 1878 but are fragmentary until 1892; the Albany gauge includes about 63% of the total flow of the Willamette River. A USGS (1999b) record for the Spokane River at Spokane, Washington, since 1891 is available. Daily flow records for the oldest Canadian gauging station (Nicholson, British Columbia, compiled by Environment Canada) began in 1903, while USGS daily records for the Snake River began in 1912 at Ice Harbor Dam in Washington.

It also is important to have an estimate of total flow from the eastern and western subbasins combined, determined as close to the mouth of the Columbia River as possible. The USGS (1999a) has measured flows at the Beaver Army Terminal (RKm 85) near Quincy, Oregon, only from 1968 to 1970 and from 1991 to the present. We have used regression analysis of daily records for Beaver, Albany, and The Dalles to hindcast a Beaver daily flow for the common period of record for Albany and The Dalles. This record is complete for 1895 to the present, and partial for 1878–1894. USGS sediment transport records for the main stem are available for 1963–1970 (Vancouver, Washington, or Beaver; Haushild et al. 1966, Hubbell et al. 1971, USGS 1999a, 1999b). USGS (1999a) sediment transport data for the Willamette River are available for 1910–1913 (some daily data are missing; Van Winkle 1914a, 1914b) and 1962–1963 (Haushild et al. 1966).

All hydrological data discussed in the remainder of this section are compiled by water year; the water year begins 1 October and ends 30 September. Flows typically have been rounded to 10 m^3s^{-1} and sediment transports to two or three significant digits. Confidence limits have not been calculated in most cases, because systematic biases may outweigh random errors.

Hydrological Effects of Climate Cycles

Climate-induced variations in Columbia River flow occur on time scales from a few years to centuries (Chatters and Hoover 1986 and 1992), and these fluctuations are important to salmonid survival. For example, indices of the Pacific Decadal Oscillation (PDO, typically 40–50 years in duration) are correlated with salmon catches since 1900 in the Pacific Northwest and the Bering Sea (Mantua et al. 1997). A cold phase of the PDO that occurred from 1945 to 1976 was generally favorable for salmonid production in the Pacific Northwest and unfavorable in the Bering Sea. The opposite circumstance prevailed during a warm phase from 1977 to about 1995. Another cold, wet phase may have commenced in the late 1990s, and salmon runs have rebounded somewhat. For purposes of this section, we define the climatic present in terms of PDO cycles as the 1945–1999 period. These PDO-related fluctuations in salmonid survival have been linked to the degree of density stratification of the coastal ocean (Gargett 1997), but survival also is influenced by conditions within the river and estuary (e.g., salinity, turbidity, and flow).

ENSO (typically 3–7 years in duration) indices are correlated with Columbia River flow (Redmond and Koch 1991) and sediment transport (Jay and Naik 2002). In addition to modifying fluvial processes, ENSO cycles may affect upwelling and primary production and therefore survival of salmonids in coastal waters.

The Columbia Basin climate response is conditioned by its position between lat. 41°30' and lat. 54°40'N, within a latitudinal band of strong response to the ENSO cycle and to the PDO cycle (Mantua et al. 1997). While the flow-per-unit area is larger in the western subbasin than in the eastern subbasin, the response to ENSO or PDO forcing varies little across the basin. Still the relatively large north-south extent of the basin brings about important differences in flow seasonality (e.g., the incidence of winter floods and timing of spring snowmelt) even within the eastern subbasin. In the next two subsections, we explore important estuarine and fluvial impacts of these climate cycles that may affect salmonids.

The lack of standard hydrological time series creates significant uncertainties about 19th century climatic conditions. The status of the PDO before 1890 remains uncertain although the fluctuations described by the PDO index have been occurring for at least 300 years and possibly for thousands of years (Finney et al. 2000). Moreover, it is difficult to find any evidence in the Columbia River flow data that a lengthy, warm PDO phase occurred between about 1849 and 1920. If the entire 1849–1920 period is considered to be a cold PDO phase, then it was much more persistent relative to cold PDO phases during the 20th century.

The results of Finney et al. (2000) may also suggest that conditions in the latter part of the 19th century were simultaneously favorable for salmonids in the Columbia River and in Alaska, a situation that has not occurred since 1900. Alternatively, estimates of Columbia River salmon abundance before 1900 are confounded by a decline in native fisheries followed by the rapid growth of commercial fisheries, and the data may not be sufficiently accurate to correlate with climate. We therefore explore correlations between climate and Columbia River hydrological processes with the caveat that climate cycles before 1900 are not well understood.

El Niño Southern Oscillation and Pacific Decadal Oscillation Effects on the Annual Flow Cycle

Variations in Columbia River flows associated with El Niño and the PDO affect habitat conditions by:

- determining what areas are wetted and potentially accessible to juvenile salmon,
- changing estuarine salinity gradients,
- influencing sediment transport processes, and
- altering the distributions of marine and freshwater species with which salmon interact.

El Niño winters in the Pacific Northwest often bring high sea level, warm air temperature, low precipitation, low snowpack, and weak subsequent spring-freshet flows (Kahya and Dracup 1993, Dracup and Kahya 1994). La Niña winters typically exhibit an opposing climate and hydrological response. The annual average flows of the Columbia and the

Willamette rivers during years with a strong El Niño winter are 91% and 92% of the long-term annual average.

During years with a strong La Niña winter the annual average flows are 110% and 111% respectively. PDO cycles also affect Columbia and Willamette flows. Cold PDO winters tend to be associated with above average flow years, while warm PDO winters are associated with below average flows (Table 6).

El Niño effects are intensified during a warm PDO phase, while those of La Niña are enhanced during a cold PDO phase (Gershunov et al. 1999). The net effect is that during an El Niño/warm PDO combination, respective average annual Columbia River flows at The Dalles and Willamette River flows are 85% and 81% of the long-term annual average; while during a La Niña/cold PDO combination, they are 111% and 119%, respectively (Figure 13). (These differences are significant at the 95% confidence limit.) El Niño effects are suppressed during the cold PDO phase as are those of La Niña during the warm PDO phase. The number of years in these extreme categories is limited.

Sediment Transport: Amplification of Climate Effects

Because sediment flow increases more than linearly with flow, the effects of climate cycles are amplified in the sediment flow. During El Niño years, annual average total sediment transports in the Columbia and the Willamette rivers are 12.7×10^6 and 1.4×10^6 mt, respectively, while in La Niña years, they are 21×10^6 and 2.3×10^6 mt, or about 65% larger. El Niño years in the warm PDO phase typically exhibit a low sediment transport (10×10^6 mt in the Columbia and 1.1×10^6 mt in the Willamette) while in the La Niña/cold PDO combination, the transport of suspended particulate matter is more than twice that during the El Niño/warm PDO years (23×10^6 mt for the Columbia and 2.2×10^6 mt for the Willamette, [Figure 14]).

Further amplification of climate effects may take place through estuarine circulation and by the detritally based estuarine food web (i.e., by the organic matter supplied during the spring freshet that supports estuarine secondary production throughout the summer and fall seasons). However, for this organic matter to be utilized by the estuarine food web, it must first be retained or trapped by estuarine circulation processes active in the estuarine turbidity maximum (ETM).

Analyses of data from fixed moorings in the estuary (Fain et al. 2001, Jay et al. 2003) suggest that particle trapping is relatively weak during extremely high river flows, because

Table 6. Effects of PDO variations the annual average flows of the Columbia and Willamette rivers.

Years	Winter type	Columbia River at The Dalles	Willamette River at Albany
1890–1921	Cold PDO	109%	102%
1922–1944	Warm PDO	86%	87%
1945–1976	Cold PDO	102%	110%
1977–1995	Warm PDO	88%	88%

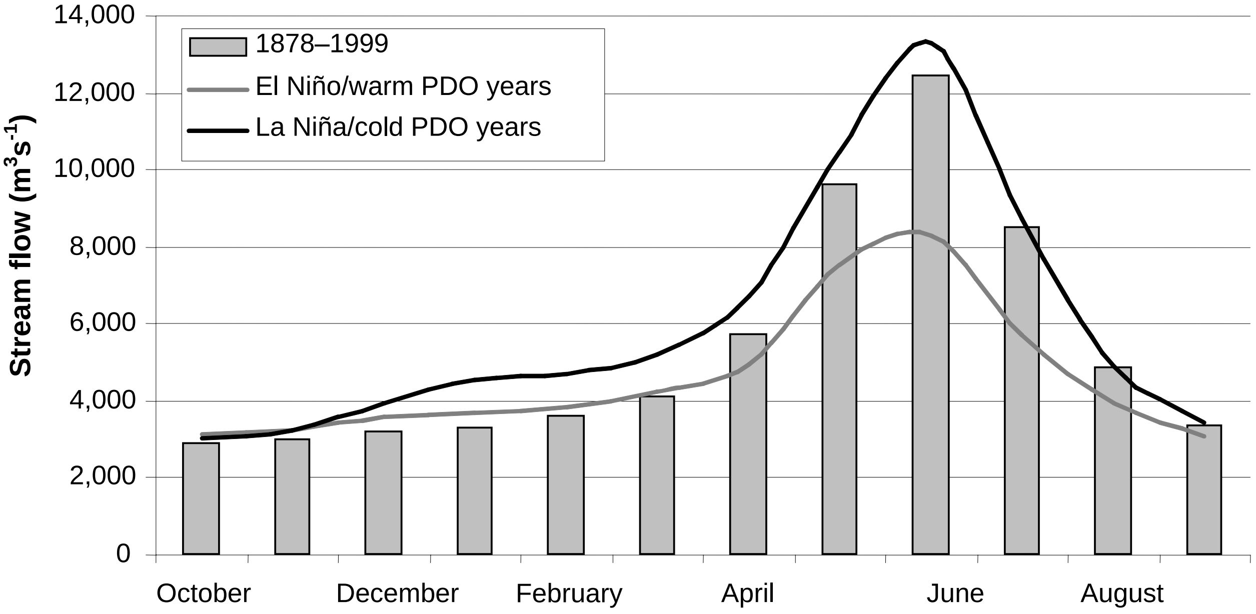


Figure 13. The ENSO/PDO response of eastern subbasin flow at The Dalles. (Data adapted from USGS records.)

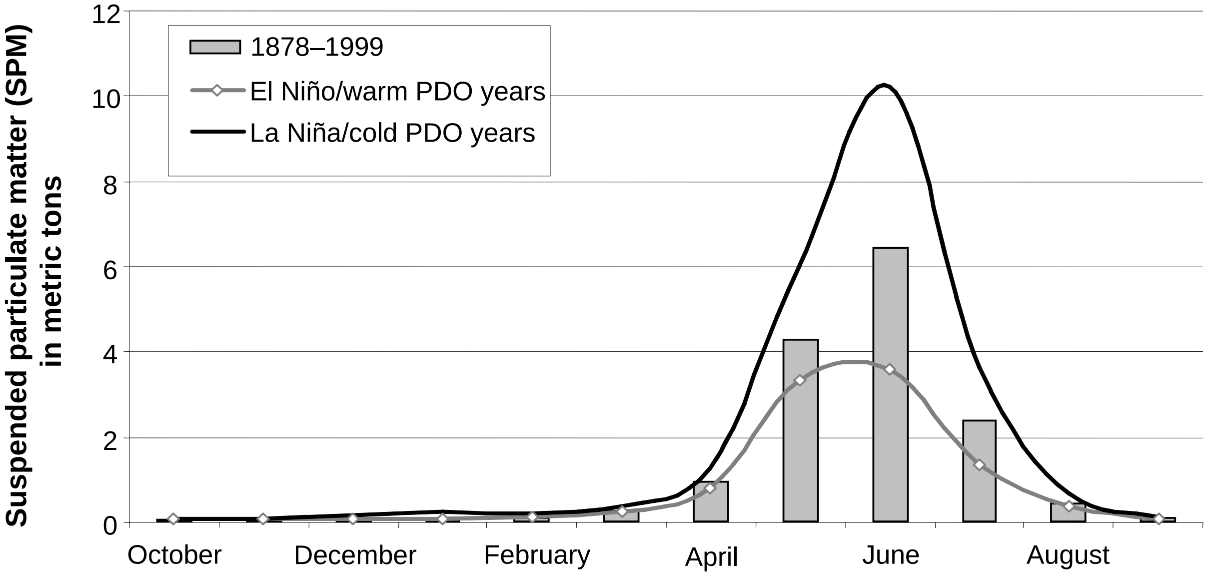


Figure 14. The ENSO/PDO response of eastern subbasin total sediment load calculated at Vancouver using flow data at The Dalles. (Data adapted from USGS records.)

extreme flows decrease the upriver extent of salinity intrusion where particles can be trapped. Decreasing river-flow levels enhance the strength of upstream flow near the bottom, enhancing particle trapping despite reduced sediment supply. Suspended particulate matter also is stored in peripheral bays during high flow periods and subsequently released to the ETM. Thus the most efficient trapping of particulates occurs during years when there is a strong spring freshet and low-to-moderate summer flows to provide a continuous supply of suspended matter, initially from the river, then from peripheral areas.

Subbasin Sources of Flow and Major Freshets

Subbasin Sources of Flow

Understanding the response of the Columbia Basin to perturbations requires attention to the diverse properties of its subbasins. There is, for example, wide variability in the percentage of flow from various parts of the basin during the spring freshet and over the rest of the water year. The Canadian part of the eastern subbasin also has a high runoff per unit area. Canada accounts for about 50% of the flow at The Dalles (37% of the flow at the mouth), but it has only 25% of the total surface area of the eastern subbasin (19% of the total surface area). The Snake River is relatively dry, with approximately 40% of the eastern subbasin surface area but only 30% of the flow at The Dalles.

In high flow years, half or more of the spring flow at The Dalles comes from Canada. During the largest known freshet (1894), the peak flow at the Grand Coulee Dam in Washington was approximately 20,500 m^3s^{-1} compared to a maximum flow of 34,800 m^3s^{-1} at The Dalles and approximately 39,400 m^3s^{-1} at Beaver (estimated). The Canadian contribution to the spring freshet has been declining since 1970 because of the long water-retention time of the dams in Canada. These dams are effective in delaying spring snowmelt flow and changing the seasonality of the flow in the upper Columbia, which in turn affects flows in the entire main stem.

An important feature of the hydrological regime is that the snowmelt occurs earlier in the Snake River area (the most southerly part of the eastern subbasin) than in the upper Columbia. The difference in the time of maximum flow among the subbasins determines freshet duration and affects the maximum flow level. In years when snowmelt occurs almost simultaneously throughout the Columbia River basin, maximum flows increase because the duration of the freshet is shorter. These conditions occur when delayed snowmelt in the Snake River subbasin coincides more closely with that of the upper Columbia River or when heavy rain accelerates snowmelt throughout the basin, as occurred in 1894 and 1948. When spring is cold, the late snowmelt in the Canadian part of the basin delays the freshet into July. Because of higher temperatures this pattern is now rarely seen in the Columbia River, but it is still sometimes observed in the Fraser River (e.g., in 1999).

Inferences from Selected Flow Histories

Spring freshets are important to the downstream migrations of juvenile salmon. Large freshets also modify habitat structure and distribution, and they thereby affect future salmon year-classes. In contrast, water quality and habitat opportunity may decline during very dry years, effects that are further exacerbated by human alterations. Thus the flow histories of extreme years convey important lessons, because salmon are most severely tested under extreme climatic conditions.

Very large freshets before modern flow regulation (i.e., before 1970) lasted 30–60 days, with the sharpness of the peak largely governed by precipitation and the relative timing of snowmelt throughout the basin. Significant winter snowmelt events occur in many winters before a major spring freshet (e.g., 1862, 1894, 1948, 1956, 1974, and 1997). These winter freshets reduce the intensity of the following spring freshet. The occurrence of major freshets, even after winter melt events, emphasizes the magnitude of the snowpack in such years.

Flow regulation and irrigation decrease spring-freshet magnitude and increase flows during the rest of year through winter draw-down of reservoirs, filling of the reservoirs during the freshet, irrigation return flow, and desynchronization of flow peaks throughout the basin. The result is a spring freshet in high flow years such as 1996 and 1997 that lasts from January to June. The effects of human manipulation (especially a weekly power-peaking cycle) are prominent during very low flow years (e.g., 1977 and 1992), when the spring freshet becomes largely an artificial event. The closest preregulation analog to such years (1926) still showed a marked annual cycle, although its intensity was reduced.

The years 1880 and 1916 play a prominent role in the present study. The model simulations described in the "Estuarine Habitat Opportunity" section (page 89) use 1880 to represent a high flow year before significant water withdrawal and navigational developments had altered the system. We chose 1880 for modeling purposes because:

- it was the earliest year for which complete flow records were available at The Dalles and for the Willamette River, and
- navigational development and irrigation withdrawal began soon afterward.

The first scientific survey of juvenile salmon in the Columbia River estuary was completed in 1916 (Rich 1920). Both 1880 and 1916 are notable for their late freshets—the latest in the 1878–2000 period—when peak flows in both years occurred in early July. Elevated flows in 1880 continued until early September leading to the highest August flows ever observed in the system. At the other extreme is the year 2000. Although the total annual flow volume was not particularly low, 2000 is unique for having the earliest recorded spring-freshet peak (23 April) because of flow regulation and a very mild winter.

Human- and Climate-induced Changes to the River-flow Magnitude and Timing

Total Annual Average River Flow from the Eastern Subbasin

Changes in annual average flow are an important integral measure of changes in a river system. In the Columbia River, about 97% of the flow from the eastern subbasin (>70% of the flow at the mouth) passes the gauge at The Dalles, making the 1878–present record useful for understanding changes in this part of the system. To separate human and climatic influences on river flow requires three distinct measures at The Dalles:

1. Observed flow—the flow observed at a gauge, available on a daily basis for 1878–present (Figure 15).
2. Estimated adjusted flow—the observed flow corrected for reservoir manipulations

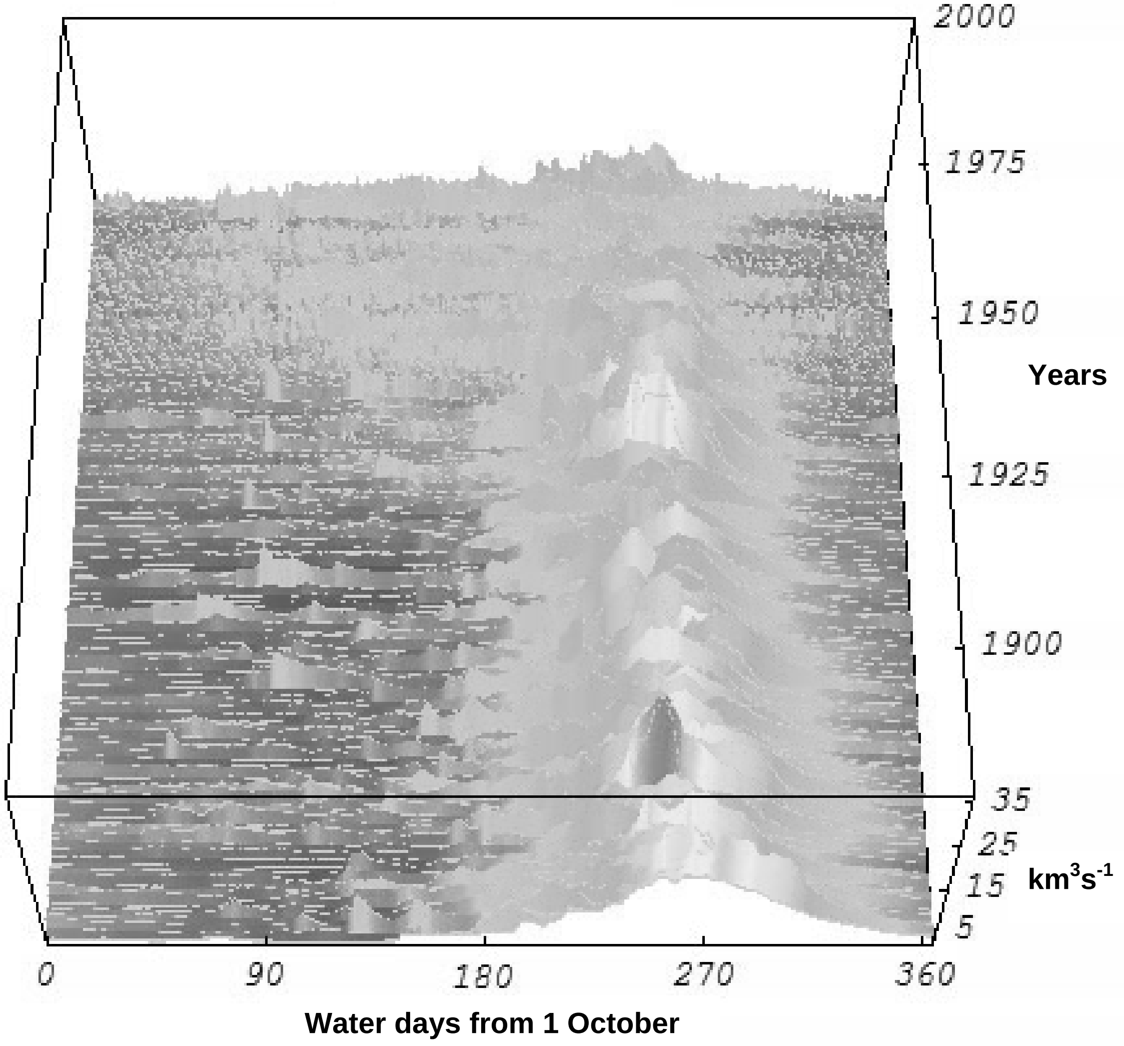


Figure 15. Daily observed Columbia River eastern subbasin flow (cubic kilometers per second) at The Dalles, 1879–1999. The daily observed flow is flow recorded off measurements by a water gauge. Peak flows are typically observed in the April to May period (black and white peaks around day 270). Peak flows appear to occur earlier in the year in the modern period (the light gray areas at the top of the figure) compared to the predevelopment era. A floor has been set at 1,500 m^{3}s^{-1} to emphasize high flow periods. (Data adapted from USGS records.)

calculated by the USGS on a monthly basis for 1878–present as per Orem (1968). We have calculated a daily adjusted flow index for the 1878–1999 period (Figure 16).

3. Estimated virgin flow—an estimate of the river flow as it would be without human alteration (i.e., the observed flow corrected for reservoir manipulation and irrigation depletion and return flows for the 1929–1989 period). These values were determined from the information tabulated by the Bonneville Power Administration (BPA 1993). We have completed the monthly virgin flow time series for the 1878–1999 period and calculated a daily virgin flow index (Naik and Jay 2004, [Figure 17]).

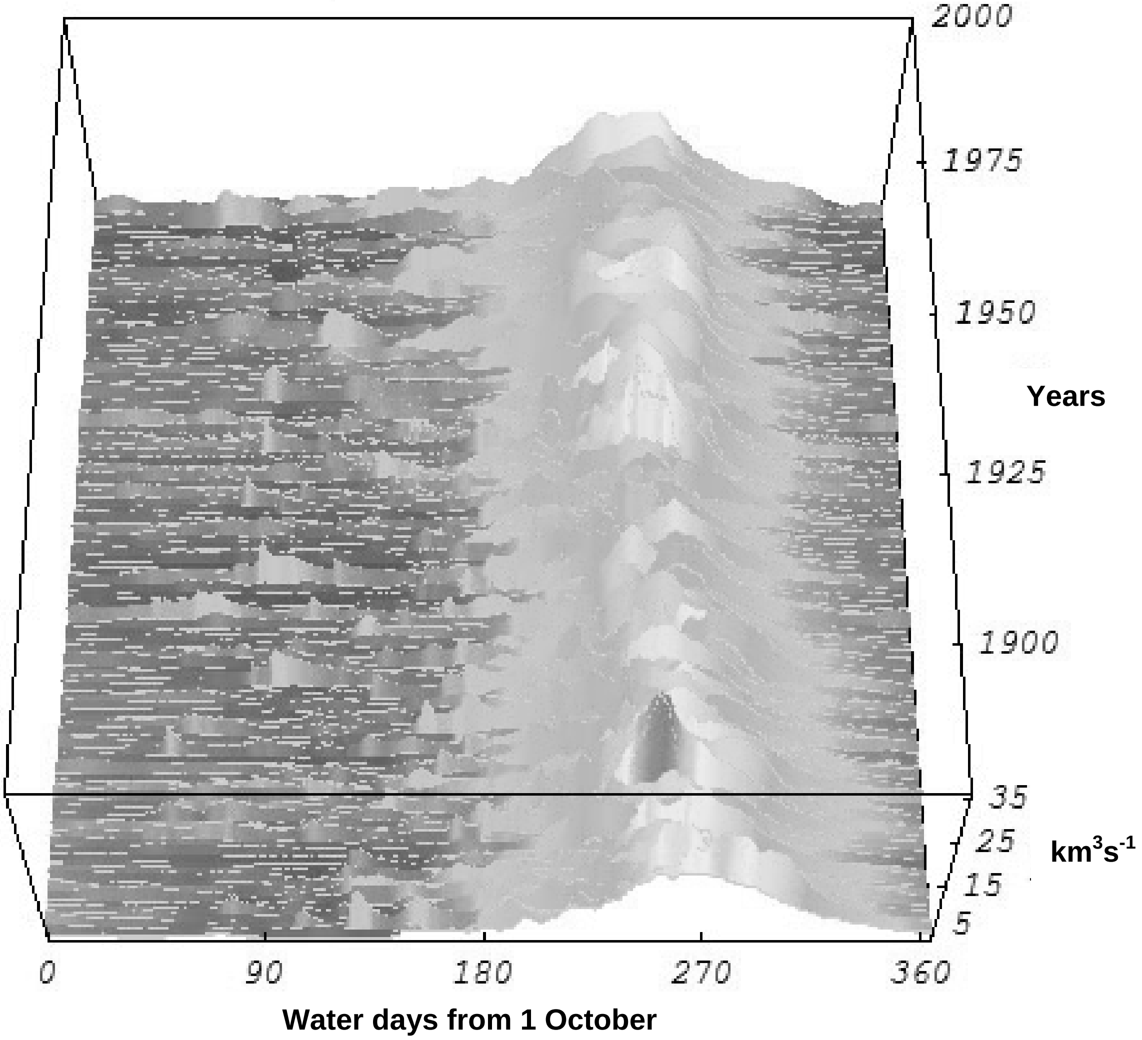


Figure 16. Daily adjusted Columbia River eastern subbasin flow (cubic kilometer per second) at The Dalles, 1879–1999. The adjusted flow is the observed flow corrected for reservoir manipulations. The daily adjusted flow diminishes after 1900 (the lack of dark areas on the peak) and ends earlier as the years progress toward 1975. A floor has been set at 1,500 m^{3}s^{-1} to emphasize high flow periods. (Data adapted from USGS data per Naik and Jay 2005.)

The effects of flow regulation and hydropower generation can be determined by comparing the observed and adjusted flows at The Dalles. The effects of water withdrawal can be determined by comparing the adjusted and virgin flows (Figure 18). The effects of climate change and land use can be estimated by examining changes in the magnitude and timing of the virgin flow over a time period (Figure 19). The total of all climatic and anthropogenic effects can be seen by comparing the virgin flow before 1900 at The Dalles to the observed flow since 1945. There is one significant caution in interpreting the calculations in this section: they are based on flow at The Dalles; however, flows at The Dalles represent the eastern subbasin only.

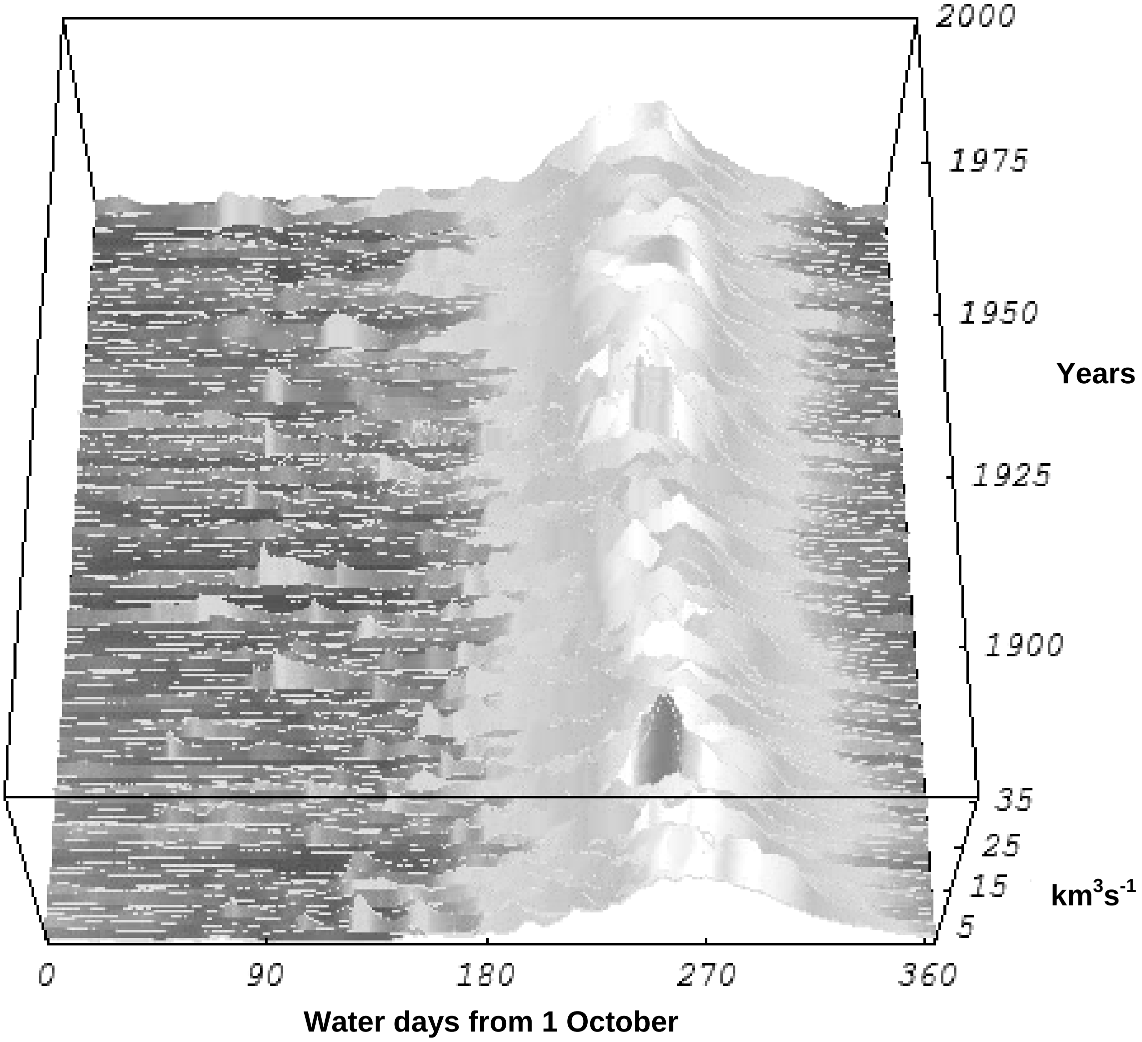


Figure 17. Estimated daily virgin Columbia River eastern subbasin flow (cubic kilometers per second) at The Dalles, 1879–1999. The virgin flow would have occurred in the absence of human manipulation. The heaviest flow (dark areas in peak) occurred before 1900. The flow diminishes and begins earlier in the spring as the years progress toward 2000. A floor has been set at 1,500 m^3s^{-1} to emphasize high flow periods. (Flow estimated from USGS data per BPA 1993 and Jay and Naik 2002.)

Virgin and adjusted flow estimates are not available for the western subbasin and anthropogenic and climatic effects on western subbasin rivers are not well understood.

It also is difficult to partition the total reduction in flow between human and climate factors, because of the need to average over climate cycles (especially the PDO) and to account for changes in flow regulation and irrigation that take place over shorter time periods. As noted previously, the present averaged over PDO cycles can be defined using the 1945–1999 period. In terms of flow regulation and irrigation, it is useful to define the post-1970 period as the present.

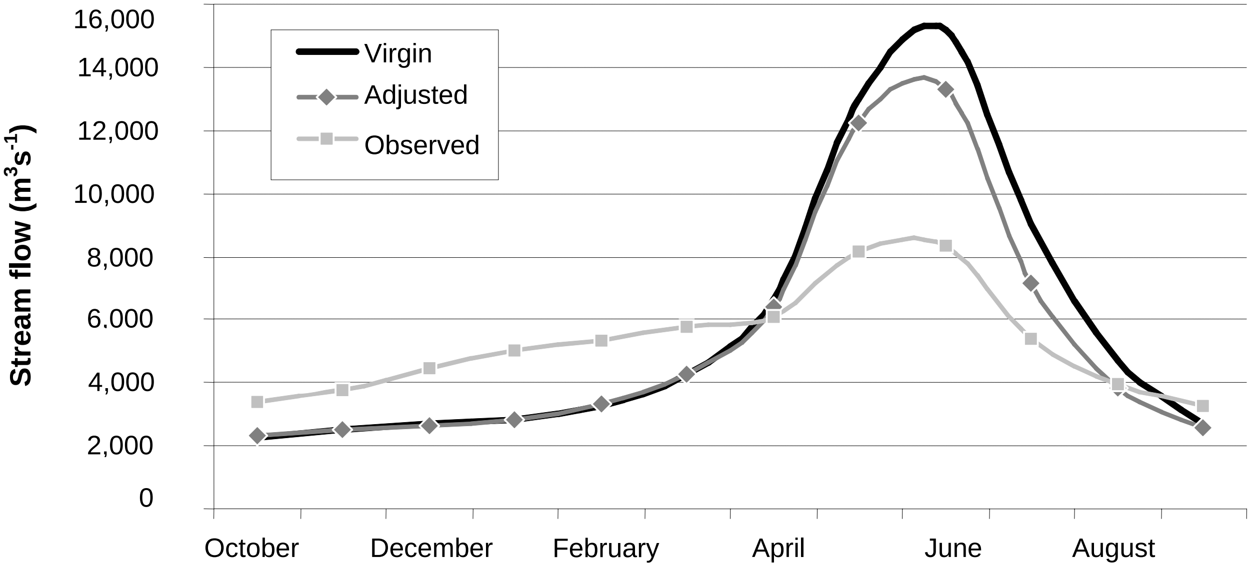


Figure 18. Comparison of the monthly averaged Columbia River eastern subbasin virgin, adjusted, and observed river-flow estimates at The Dalles, 1970–1999. (Data adapted from USGS records.)

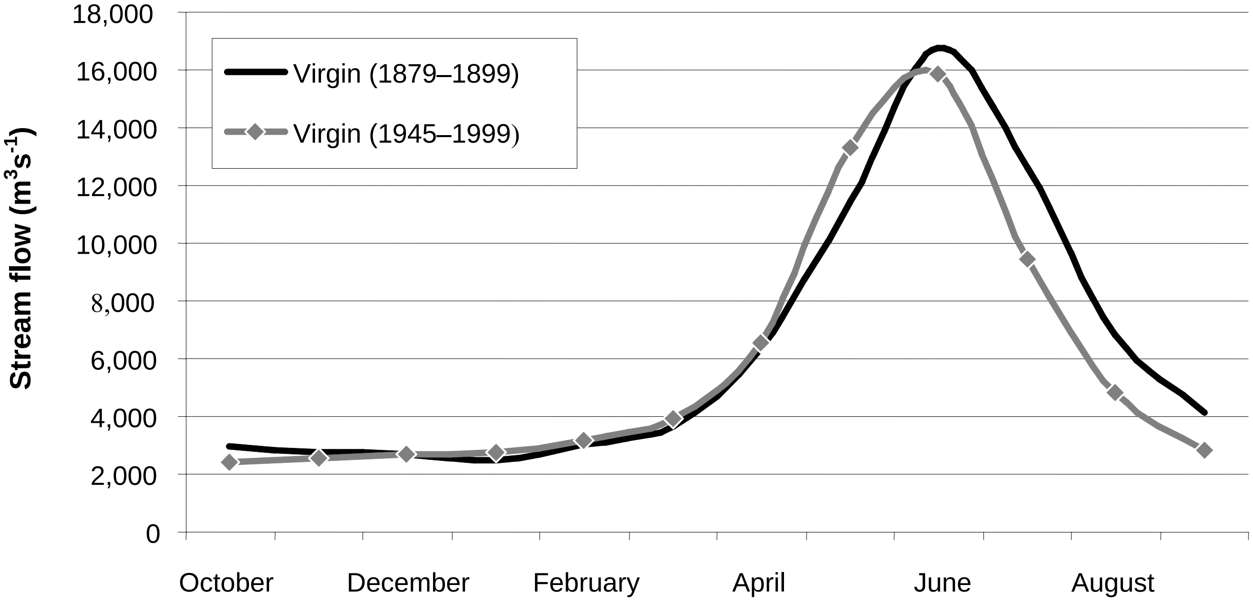


Figure 19. Comparison of the monthly averaged Columbia River eastern subbasin virgin river flow at The Dalles between 1878–1899 and 1945–1999. (Data adapted from USGS records.)

The mean annual average Columbia River virgin flow at The Dalles has decreased approximately 7.4% or 470 m^3s^{-1} from 6,320 m^3s^{-1} for 1879–1899 to 5,850 m^3s^{-1} for 1945–1999. This represents the flow decrease because of climate change (Figure 19). If annual average flow is estimated from the maximum freshet flow each year for 1858–1978, then annual average flow for 1858–1899 was 6,280 m^3s^{-1}, only slightly different from 1879–1899. Glacial retreat during the last half of the 19th century (following the end of the Little Ice Age) may have played a role in the observed high 19th century virgin flow in the Columbia River, but it is unlikely to account for most of the difference between the present and the late 19th century. Thus the last half of the 19th century had a rather different (wetter and cooler) climate regime, and very high spring flows occurred in many years between 1858 and 1900.

The 1945–1999 annual average loss because of water withdrawal for irrigation (difference between virgin flow and flow adjusted for reservoir manipulation) is 440 m^3s^{-1} or approximately 7% of the 19th century virgin flow. The 1970–1999 annual average loss because of water withdrawal for irrigation is 470 m^3s^{-1} or approximately 7.4% of the 19th century virgin flow.

The total reduction of annual average flow (difference between 19th century virgin flow and 1945–1999 observed flow of 5,360 m^3s^{-1}) is 960 m^3s^{-1} or 15.2% (Figure 19). This is larger than the climate change (7.4%) plus irrigation withdrawal (7.0%). The discrepancy (about 0.8% of the original virgin flow) represents an uncertainty level related to the different averaging periods used in the estimates. If we consider the 1970–1999 period as the present, then the total reduction is somewhat larger, 1,070 m^3s^{-1} or 16.9%. We apportion this net change as follows: climate change (8.9%), irrigation depletion (7.4%), and uncertainty (0.5%). The longer averaging period (1945–1999) more realistically represents climate effects; the shorter period (1970–1999) more realistically represents the impacts of the present management regime.

The annual average flow is not only reduced by human manipulations, but the year when flow occurs may be changed by the storage time of water in reservoirs. The total average flow of the Columbia River at The Dalles is 171.2 cubic kilometers per year (km^3year^{-1}) whereas the storage capacity is 77.7 km^3, yielding a ratio of storage capacity to annual flow of 0.45. Regulation of river flow does not normally result in large interannual transfers of flow, as it would in a basin with a larger storage capacity relative to the total annual water production (e.g., the Colorado River). Nonetheless interannual transfers of plus or minus 370–790 m^3s^{-1} occurred in 1974, 1976–1978, and 1992. These interannual transfers decrease the interannual variability of the flow.

The above discussion has not considered the consequences of land use, especially deforestation, on river flow. Deforestation may alter the hydrologic cycle by decreasing transpiration and accelerating snowmelt, thereby increasing total flow and altering its timing. Matheussen et al. (2000) suggested that these factors have modified eastern subbasin flow seasonality, changing individual average monthly flows by as much as 5–10%. Still, the change in annual average flow suggested by Matheussen et al. is small relative to the current irrigation depletion; the net change in flow over a time period is only plus 1–2%. Nonetheless deforestation may have contributed to changes in the flow cycle in certain months by requiring larger alterations to meet specific flow targets or the needs of power generation, even though the effect on annual average flow is small. Our virgin flow estimates are largely unaffected by changes in land use and deforestation, because these changes would have been compensated by reservoir flow adjustments. If changes because of deforestation are taken into account, the actual reduction in virgin flow because of climate change is more than 7.4%; however, a decrease of 8–9% may be more accurate. These considerations might modestly increase the total estimated flow decrease of approximately 15% (1945–1999) or 17% (1970–1999) by 1-2%.

Eastern Basin, Spring-freshet Magnitude and Timing

The changes in annual average flow are only a small part of the total hydrological changes in the Columbia River. Seasonal changes, particularly those in spring-freshet timing and magnitude, have been much larger than those in annual average flow. Spring freshets are extremely important for juvenile salmonids, because high flows (especially overbank flows) provide habitat, limit predation by increasing turbidity, and maintain favorable water temperatures during the spring and early summer. Organic matter supplied by the river during the freshet season is also a major factor maintaining a detritally based food web, centered in the ETM.

Flows from the Columbia River eastern subbasin (the flow measured at The Dalles) are primarily driven by spring snowmelt, although rain-on-snow freshets occur in some winters. Before 1900, the highest flows typically occurred during May–July. Monthly Columbia River virgin flows at The Dalles for 1879–1899 were 11,480 m^3s^{-1} for May, 16,760 m^3s^{-1} for June, and 12,600 m^3s^{-1} for July. The corresponding figures for 1945–1999 were 13,300 m^3s^{-1} for May (+15.9%), 15,840 m^3s^{-1} for June (–9.5%), and 9,420 m^3s^{-1} for July (–25.2%).

The decrease in July flows and the increase in May flows have been caused by the earlier onset of spring freshets (Figure 20 and Figure 21). Also the May–July average virgin flow for 1879–1899 was 13,610 m^3s^{-1}, while for 1945–1989 it was 12,850 m^3s^{-1} (–5.6%). This represents the freshet-season flow decrease because of climate change. Note that the January–July virgin-flow average for 1879–1899 was 8,050 m^3s^{-1} compared to 7,850 m^3s^{-1} for 1945–1989, a decrease of only 2.5%. Thus most of the loss of freshet flow represents flow that now occurs during winter, early spring, or late summer and fall.

The modern freshet-season flow decrease caused by water withdrawal can be determined from the 1970–1999 differences between the monthly Columbia River virgin and adjusted flows at The Dalles. The virgin-flow reductions were 750 m^3s^{-1} for May (5.7%), 1,900 m^3s^{-1} for June (12.5%), and 1,890 m^3s^{-1} for July (20.8%). The total May–July seasonal water-withdrawal decrease was about 10.5%.

The present freshet-season flow decrease because of flow regulation can be determined from the 1970–1999 differences between the monthly Columbia River adjusted and observed flows at The Dalles. These virgin-flow reductions were 4,100 m^3s^{-1} for May (31.6%), 4,920 m^3s^{-1} for June (32.4%), and 1,790 m^3s^{-1} for July (19.8%) for the period. The total freshet-season flow decrease because of flow regulation was 3,600 m^3s^{-1}, 29.1% of the present spring virgin flow and 33.1% of the present spring-adjusted flow. Flow regulation is clearly the source of the largest reduction in spring flow.

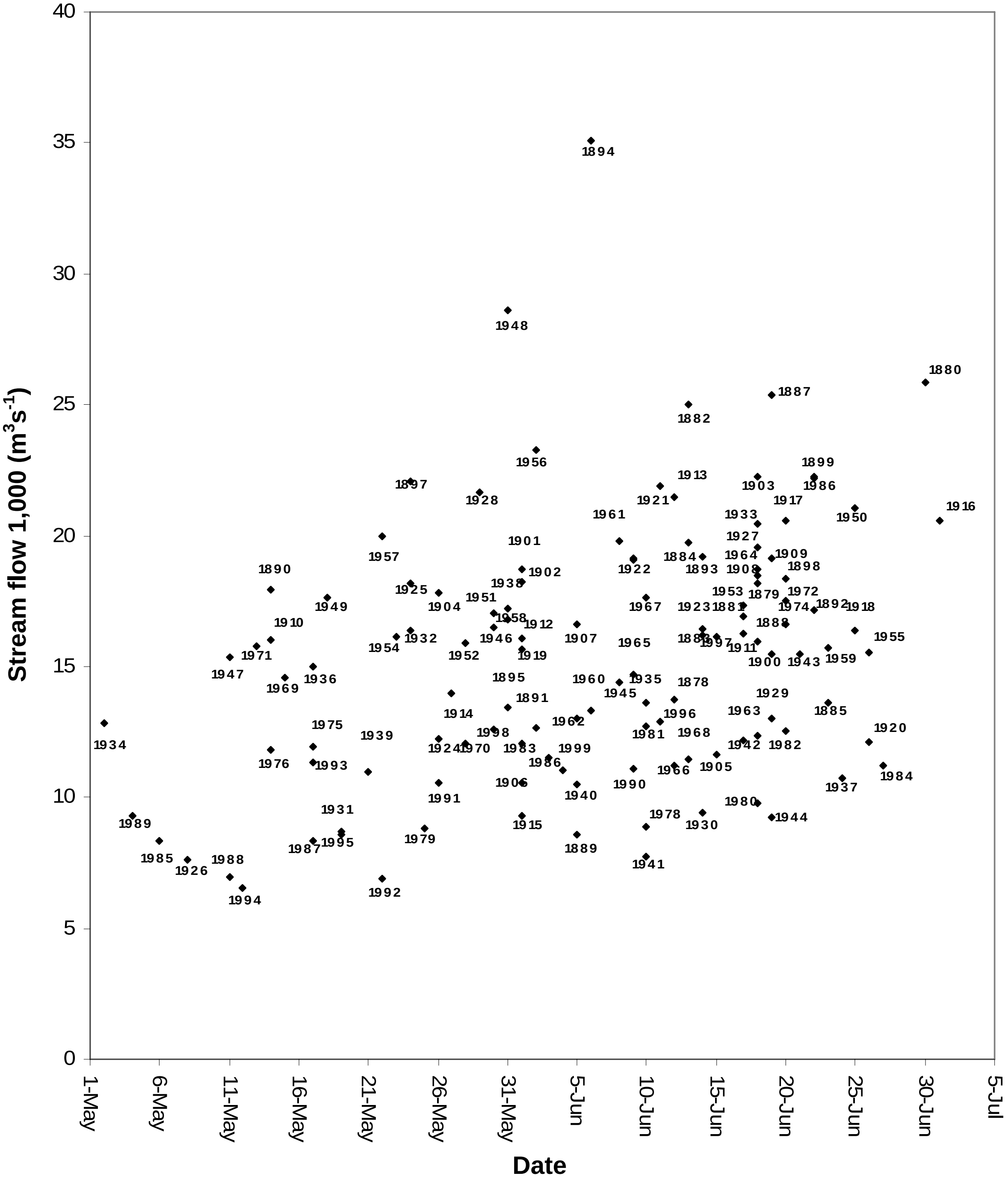


Figure 20. Seasonal magnitude and timing of Columbia River eastern subbasin freshets at The Dalles, 1878–1999. (Data adapted from USGS records.)

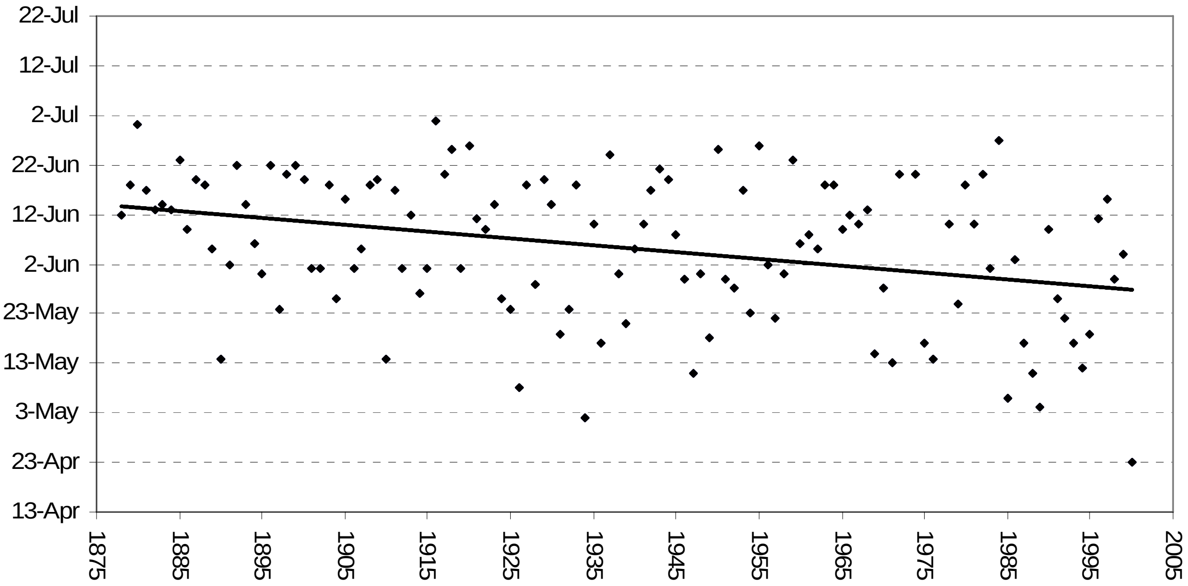


Figure 21. A linear fit to of peak freshet day versus year; the spring freshet now occurs about two weeks earlier than in the 19th century. (Data adapted from USGS records.)

The total reduction in freshet-season (May–July) mean flow because of climate change, irrigation depletion, and flow regulation was 5,870 m^3s^{-1}, 43% of the virgin flow for this period. The present freshet season flow of 7,740 m^3s^{-1} was about 148% of the current annual average flow. In contrast, 19th century freshet flows were approximately 215% of the contemporary mean.

The reduction in peak flows of freshets has been slightly larger than that of the freshet season as a whole. The observed maximum annual daily spring-freshet flow for 1858–1899 was 19,300 m^3s^{-1}, which is close to virgin spring-freshet magnitude because water withdrawals during the 19th century were small. Present (1970–1999) observed annual maximum daily spring-freshet flow was 10,870 m^3s^{-1}, 44% less than before 1900. Peak freshet flow for 1945–1999 was 13,530 m^3s^{-1}, 30% less than before 1900. Freshet reduction was less effective before 1970.

Because of the disparate time scales involved, it is difficult to separate reductions in daily maximum flow caused by climate, deforestation, irrigation, and flood control. The climate-change component is not the largest factor, given the small climate-induced change in the May–July average flows. Present irrigation withdrawal during the spring-freshet season is normally less than 1,800 m^3s^{-1}, also small relative to the freshet reduction. Most of the loss in maximum spring-freshet flow, therefore, is because of flow regulation. Flood-control reductions of more than 10,000 m^3s^{-1} occur in high flow years such as 1974 and 1997 (Figure 22). The original maximum daily flow 305% of the mean, whereas this figure has been reduced to 205% at present.

Still the role of climate change in reducing freshet magnitude over the past 140 years should not be totally neglected. Even though climate-induced changes in annual average flow

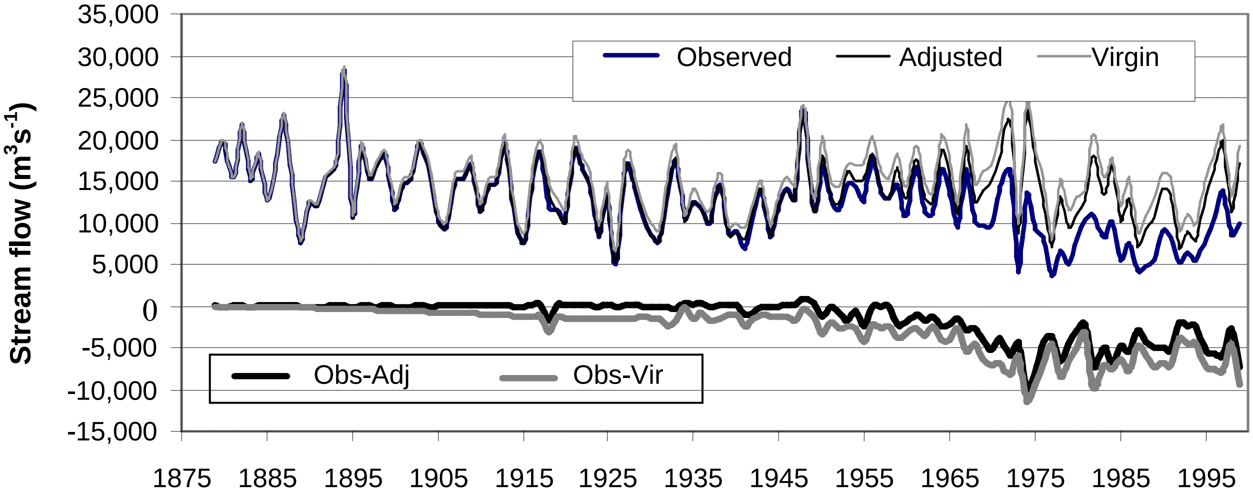


Figure 22. Reduction of the monthly mean June flow. (Data adapted from USGS records.)

have been modest, the annual flow cycle has changed also, probably because of a combination of higher average air temperatures and deforestation. The Columbia River has shifted from a climate regime (before 1900) when winter freshets in the eastern basin were unusual to a climate regime when substantial flow events now occur in many winters.

One result of climate change is that the incidence of very large spring freshets was greater during the last half of the 19th century. Peak-flow information is available for only 43 years in the 19th century (1849, 1858–1999), yet 10 of the 14 largest known freshets occurred before 1900. This compilation is based upon estimated virgin daily flow, so that direct human manipulation is not the reason for the difference. Similarly, four of the five largest known freshets in the Willamette River occurred in the 19th century.

The timing of the maximum spring-freshet flow also has changed (Figure 21). Maximum daily spring-freshet flow now typically occurs at about water-year Day 242 (29 May), whereas maximum flow occurred at about water-year Day 256 (12 June) in the 19th century, a change of about two weeks. In terms of the phase of the annual flow fluctuation (as determined by wavelet transformation of the flow data), the freshet is about a month earlier. Part of this change is because of climate warming, but prerelease of water for flood control before the spring freshet is also a component. Irrigation withdrawal usually peaks in June, which tends to further curtail the freshet.

The relative size of these three effects on freshet timing cannot be determined. However, the very early 2000 spring-freshet peak on 23 April (the only April freshet ever recorded) occurred largely as the result of flow regulation.

Changes in Western Subbasin Flows

The eastern subbasin flow at The Dalles described previously accounts for about 75% of the total flow to the estuary. Flows in the Willamette River are typical of the remaining 25% from the western subbasin. The Willamette is the largest river in the western subbasin, with approximately 60% of the western subbasin flow, or 15% of the total flow for the basin. Climate influences on the Willamette are similar to those on other western subbasin tributaries (e.g., the Cowlitz, Kalama, and Lewis rivers in Washington) draining the west side of the Cascade Mountains, although the Cowlitz has a larger contribution from seasonal snowpack, and anthropogenic effects are system-specific.

The Willamette River responds primarily to winter rainfall and melting of recently deposited snow, with only modest storage of water in seasonal snowpack and glaciers. The largest freshets in the system are caused by winter, rain-on-snow events. The Willamette River basin is much smaller than the eastern subbasin; its flows are not as heavily regulated and there are no mainstem storage dams.

For these reasons, and because the Willamette Basin area is small relative to that of synoptic weather events, Willamette River flows are much more variable on short time scales than those at The Dalles (Figure 23).

The observed annual average Willamette River flow at Albany has decreased from 460 m^3s^{-1} for 1893–1900 to 418 m^3s^{-1} for 1945–1999 (9.5%) and to 390 m^3s^{-1} for 1970–1999 (14.8%). It is not currently possible to separate the components into losses associated with climate and water withdrawal, but irrigation withdrawal was small before 1900 (Sedell and Frogatt 1984). Still it appears that historical changes in annual average flow have been smaller in the Willamette than in the eastern subbasin.

The seasonality of Willamette River flow at Albany has been altered by climate change, the irrigation cycle, and flow regulation for flood control (Figure 24). Late summer to early winter flows (August–December) have been augmented (comparing the historic and modern flows), likely by irrigation-return flow and by prerelease of any surplus water before winter. Average monthly flows during the January–July periods have decreased, especially those in January and February, when the reduction has exceeded 120 m^3s^{-1}, out of the original approximately 920 m^3s^{-1}. The decrease in mid-winter average (and extreme) flows is probably because of a combination of climate effects and flood control. The difference between the historic and modern flows peaks again in May at greater than 120 m^3s^{-1}. Irrigation and storage of water for summer power generation are likely reasons for the spring-flow decrease. However, the seasonal snowpack also may be smaller. The effects of land-use changes on Willamette River flow are unknown.

River Flows at the Head of the Estuary

The best measure of total mainstem freshwater input at the head of the estuary is the Columbia River flow at Beaver. Flow properties at Beaver are the sum of those for the eastern and western subbasins (Figure 25). The average estimated observed annual flow (1892–1999) at Beaver is 6,960 m^3s^{-1}. It is not possible to separate climate, flow regulation, and water-withdrawal effects on the flow at Beaver, but the average flow is now substantially lower. The average annual flow for 1892–1902 was roughly 8,300 m^3s^{-1}. Reflecting the alteration of eastern basin flows, the spring freshet at Beaver has become longer, weaker, and earlier, while winter flows are less sharply peaked than before flow regulation. Monthly average winter flows

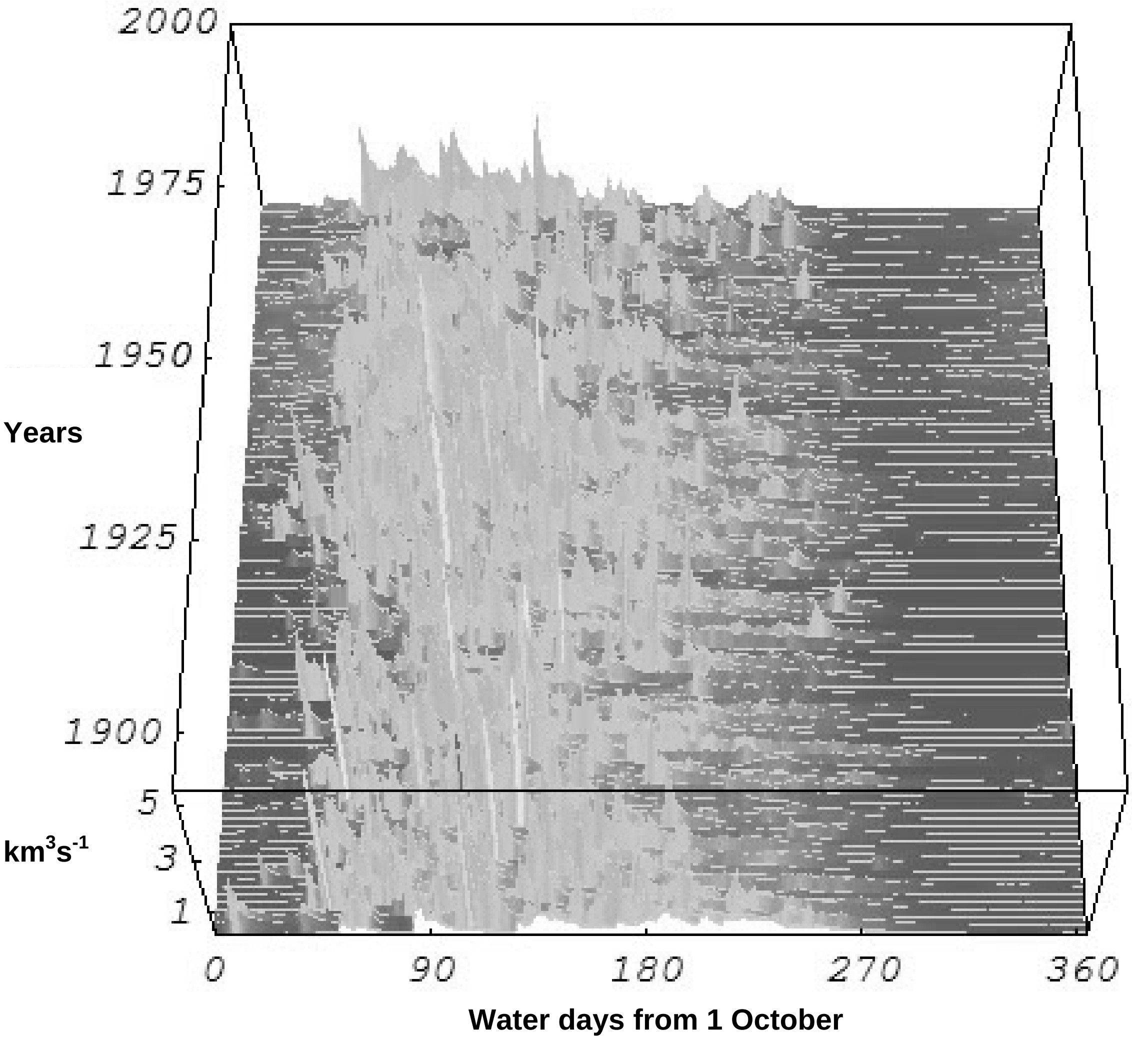


Figure 23. Observed daily Willamette River flow (cubic kilometers per second) at Albany, 1893–1998. This flow is representative of the western subbasin. Almost all of western subbasin flow is from rain events (peak flows in the winter), while eastern subbasin flow is mainly from the melting snowpack (peak flows in the spring). A floor has been set at 200 $m^3 s^{-1}$ to emphasize high flow periods. (Data adapted from USGS records.)

are slightly larger than before 1900 (Figure 26). There are no long-term sediment transport estimates available for Beaver.

Flows from Estuary Tributaries

The flow at Beaver is not the total flow of the Columbia River. Several smaller rivers enter the estuary seaward of Beaver (e.g., the Elochoman and Grays rivers in Washington and the Youngs and Lewis and Clark rivers in Oregon). These river basins have very high runoff intensities, but they contribute an estimated annual average of only 3% of the total flow at the river mouth, or approximately 230 m^3s^{-1} (Orem 1968). Their contribution during winter storms is probably much higher, but it has not been systematically assessed.

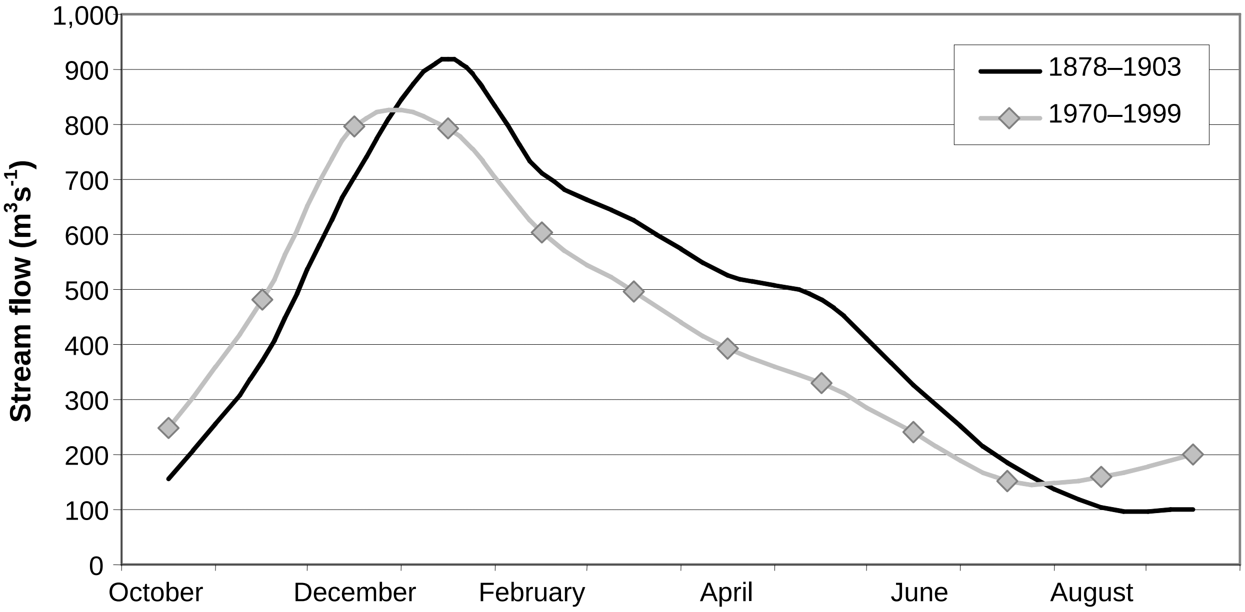


Figure 24. Historical changes in the annual flow cycle of the Willamette River at Albany, 1878–1903 (from 1878 to 1894 not all daily values are present) versus 1970–1999. (Data adapted from USGS records.)

Little is known regarding historical changes to the hydrological properties of the estuary tributaries, and no systematic sediment-transport records are available. Downstream transport of logs to tidewater during early logging operations severely disrupted several of these streams.

Total Columbia River Flow at the Mouth

The total annual average flow at the mouth of the Columbia River can be estimated by adding the estuary tributary flow to the long-term average for Beaver. The result is approximately 7,300 m^3s^{-1} for 1892–1999. This is somewhat smaller than the figure (7,720 m^3s^{-1}) given by Orem (1968) for two reasons:

1) Orem used primarily data from a cold PDO phase of elevated flows (1943–1957), and
2) the average observed flow has decreased slightly since Orem's work was published.

Finally, the value of the Columbia River flow at the mouth prior to 1900 was probably about 8,500 m^3s^{-1}; it decreased to about 7,080 m^3s^{-1} (1970–1999).

Human- and Climate-induced Changes in Sediment Transport

Sediment transport processes are a vital determinant of habitat conditions for salmon and other species in the estuary. The organic component of the fine sediment supply (silts and clays) supports a detritus-based food web that now provides the bulk of estuarine secondary productivity in the system (Simenstad et al. 1990a, 1994). The turbidity caused by fine sediment

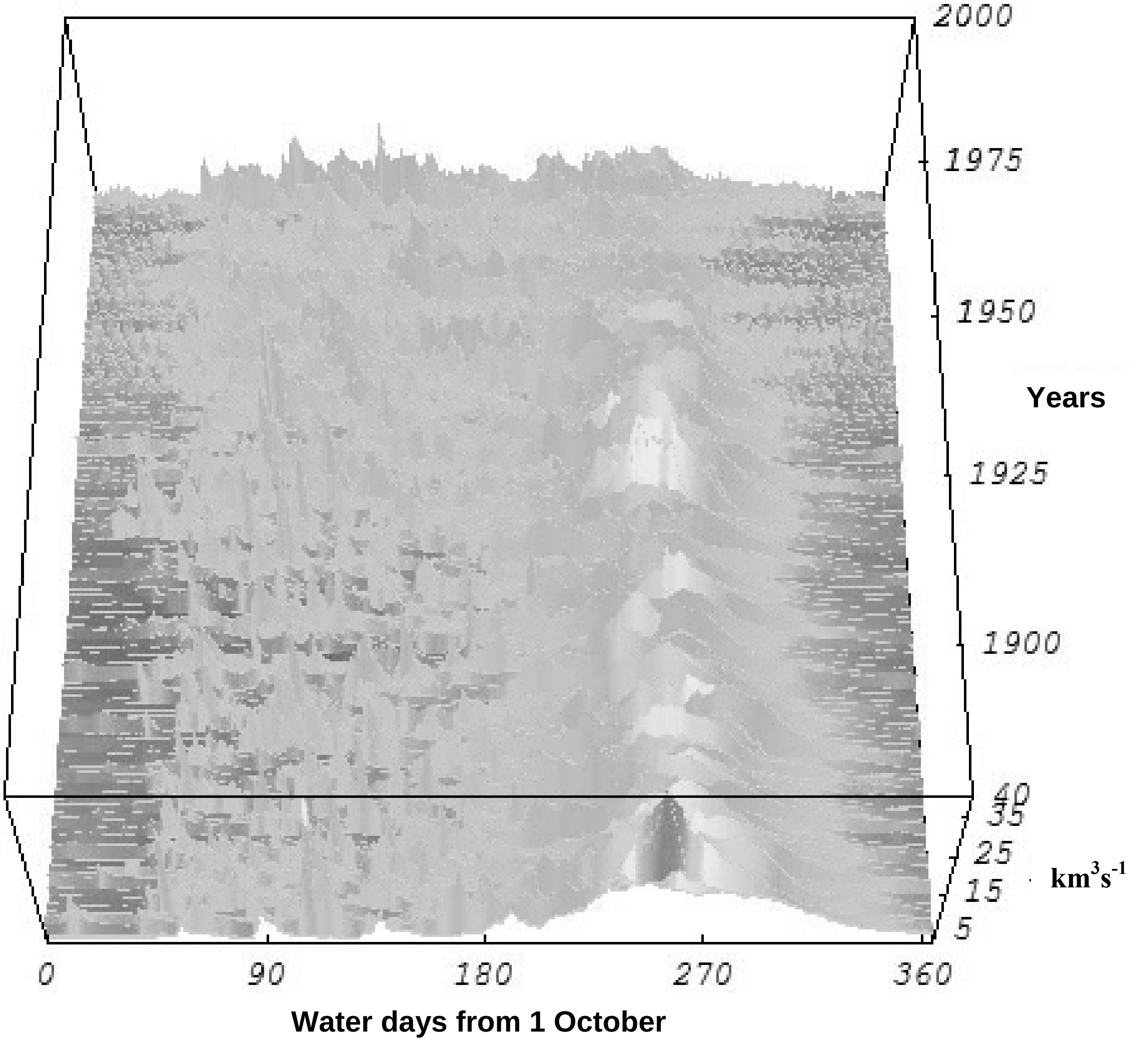


Figure 25. The combined eastern and western subbasin flows: estimated observed daily Columbia River flow at Beaver, 1892–1999. Note the combination of characteristics derived from the eastern and western subbasins (light gray areas). Peak flows are typically observed in the April–May period (black and white peaks around day 270). Peak flows appear to occur earlier in the year in the present period (the wide gray area at the top of the figure) compared to the predevelopment period (before 1900). A floor has been set at 1,500 m^3s^{-1} to emphasize high flow periods. (Data adapted from USGS records.)

may hinder predation on juvenile salmonids, but excessive levels may be injurious to juveniles and damage spawning habitat. The coarser fractions (sands and gravels) are critical to natural habitat construction in the estuary and to maintenance of spawning habitat higher in the basin. During the past century, dredging and disposal of sands and gravels have been major causes of estuarine habitat loss. For scientific reasons, it is important to distinguish between the fine and coarse-sediment fractions. For methodological reasons, sediment transport is reported in terms of total load (all fractions) and sand, which includes gravel.

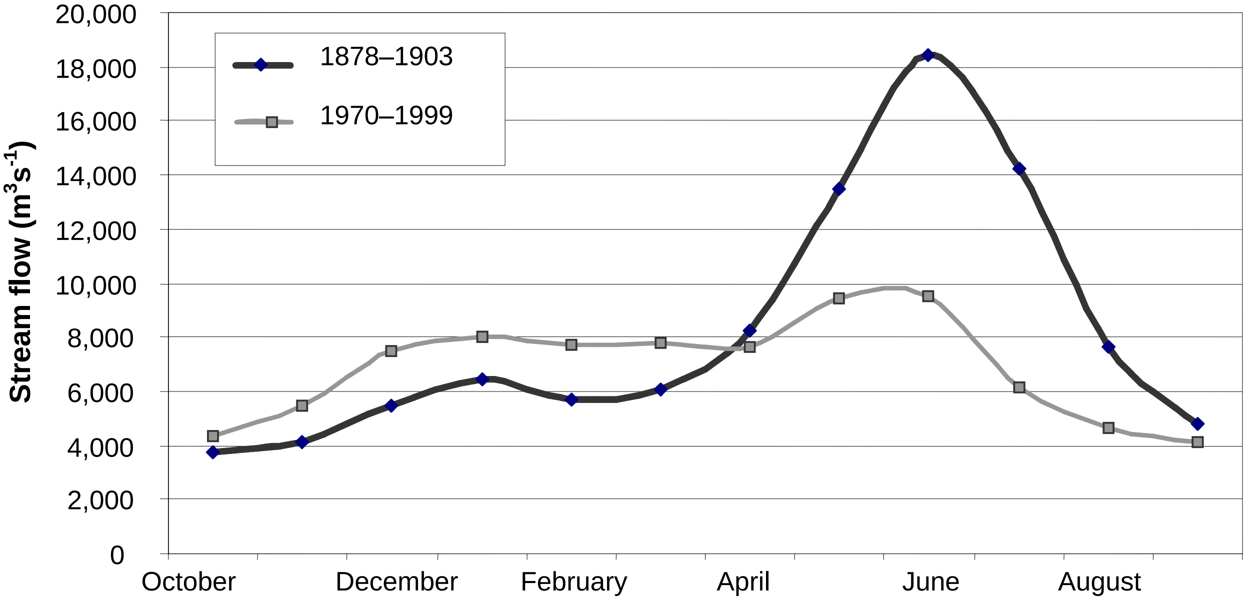


Figure 26. Changes in the annual flow cycle of the Columbia River at the Beaver Army Terminal, 1878–1903 (from 1878 to 1894 not all daily values are present from Albany) versus 1970–1999. (Data adapted from USGS records.)

Daily sediment-transport data (at Vancouver) for the eastern subbasin are available only for 1963–1970. Therefore, we have hindcast total load and sand transport at Vancouver for the entire period (1878–1999) of the daily flow record at The Dalles, estimating the sand fraction based on measurements described in Haushild et al. (1966). This calculation has been carried out for the observed and virgin flow (Figure 27). Willamette River total load has been hindcast for 1892–1999 on the basis of 1910–1913 and 1962–1963 sediment-transport data.

Estimated sediment supply for the two systems assumes that land use and channel development have not materially altered sediment transport. Sand movement is transport limited; material is available on the bed and will move whenever flow conditions are suitable. We expect that the sand-transport estimates, therefore, are relatively accurate, at least within the limited flow range of the data set used to calibrate sand transport. Transport of fines, however, is supply limited; normally, the capacity to move the material is greater than the supply.

Fine sediment transport can only be hindcast under the assumption that the supply of these materials has not changed. In fact, timber harvest, agriculture, and urban development have likely affected the supply of fine material. The available evidence suggests that the supply of fines depends on the source and timing of the flow. Still a consistent estimate of sediment transport unaffected by land use has some advantages. It is useful to compare the contributions of climate and human manipulations to the flow cycle.

The effects of climate change on total sediment supply can be determined from historical changes in sediment transport at Vancouver associated with virgin flow at The Dalles (Table 7). Combining the hindcast total load (sand + finer fractions) for 1879–1899 with the annual average

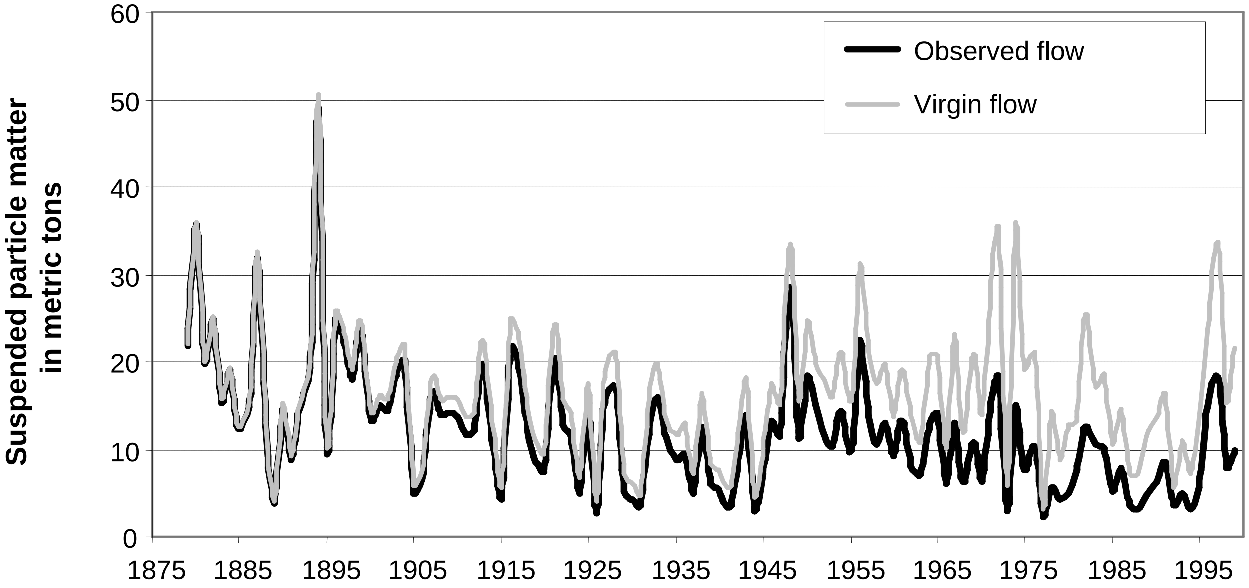


Figure 27. Hindcast total sediment load (metric tons) for the Columbia River eastern basin calculated at Vancouver from the observed flow (cubic meters per second) and estimated virgin flow. (Observed-flow data adapted from USGS records; virgin-flow data adapted from Jay and Naik 2003 and BPA 1993.)

Table 7. Estimated effects of climate change on total sediment transport and on sand transport (at Vancouver) based on virgin-flow estimates at The Dalles.

Flow condition	**Period of record**	**Total sediment transport ($\times 10^6$ mt)***	**Sand transport ($\times 10^6$ mt)***
19th century	1879–1899	20.5	10.9
	1858–1878	21.2	9.8
	1858–1899 (mean)	20.8	10.4
20th century	1945–1999	17.2	8.3
Change (because of climate)	(1858–1899)–(1945–1999)	–3.6 (–17%)	–2.1 (–20%)

* Average annual sediment transport ($\times 10^6$ mt) estimated from maximum daily flows.

sediment transport (estimated from annual maximum daily flow) for 1858–1878, we estimate annual average sediment transport for 1858–1899 was approximately 20.8 × 10^6 mt. Compared to similar estimates for 1945–99 virgin flows, total sediment transport decreased approximately 3.6 × 10^6 mt (≈17%) because of climate change. This is a considerably larger decrease than the climate-driven change in flow for two reasons:

1) sediment transport varies with a power n of the flow (n is approximately 2.5), and

2) decreased mean flow also reflects reduced flow variability and frequency of high flow days that transport most of the total load.

Climate change similarly accounted for an estimated decrease of 2.1 × 106 mt (≈20%) in annual average sand transport from 1858–1899 to 1945–1999 (Table 7). The percentage decrease in sand transport is larger than that in total sediment transport, because the percentage of sand in the total sediment load increases as flow increases.

The total change in sediment transport (including the effects of human manipulation of flow such as dams and irrigation) on sediment supply can be estimated by subtracting average annual sediment transport under virgin flows with similar estimates for observed flows (Table 8). The difference between annual average sediment transport at Vancouver for 1858–1899 virgin flow and for 1945–1999 observed flow was 10.8 million × 10^6 mt (52%) of the 19th century sediment transport. The changes are larger if we consider sediment transport for observed flows after 1970, when the Columbia River became fully regulated. The difference between annual average sediment transports for the 1879–1899 virgin flow and 1970–1999 observed flow is approximately 12.5 × 10^6 mt (≈61.5%) of the 19th century sediment transport.

Decreases in sand transport because of flow manipulations are similarly high (Table 8). The sand transport associated with the 1945–1999 observed flow was approximately 3.2 × 10^6 mt, approximately 7.7 × 10^6 mt less than the 1879–1899 virgin flow (≈71% of the 19th century sand transport). Because sediment transport is related to flow in a nonlinear way, it is not possible to apportion the reduction in sediment transport precisely between climate change, water withdrawal, and flow regulation. The largest single factor is reduction in spring-freshet flow for power generation, flood control, and irrigation.

The reduction of western subbasin winter freshets by climate change and flow regulation also has decreased sediment transport. The Willamette River total sediment transport hindcast for 1893–1903 was 2.4 × 10^6 mt; whereas it was only 1.5 × 10^6 mt for 1970–1999, a reduction of

Table 8. Long-term changes in total sediment and sand transport (at Vancouver) based on hindcast virgin flows and observed flows at The Dalles.

Flow conditions	**Period of record (total sediment transport**	**Total sediment transport ($\times10^6$ mt)***	**Period of record (sand transport**	**Sand transport ($\times10^6$ mt)***
Virgin flow	1858–1899	20.8		
Observed flow	1945–1999	10.0		
Long-term change	(1858–1899)–(1945–1999)	–10.8 (–52%)		
Virgin flow	1879–1899	20.5	1879–1899	10.9
Observed flow	1970–1999	8.0	1945–1999	3.2
Long-term change	(1879–1899)–(1970–1999)	–12.5 (–61.5%)	(1879–1899)–1945–1999)	–7.7 (–71%)

* Average annual sediment transport ($\times10^6$ mt) estimated from maximum daily flows.

approximately 35%. It is not possible to separate human and climate effects in this estimate. The Willamette River channel has been more heavily altered (by straightening and elimination of backwater areas, possibly increasing transport capacity) than even the Columbia River channel. The effects of agriculture and urban development also have been pervasive in the Willamette Valley. This may indicate that hindcast estimates are less useful in the Willamette than the Columbia. Still no systematic difference was found between the 1910–1913 and 1962–1963 sediment transport rating curves for the Willamette.

Human and Climate Effects on Disturbance Frequency

The frequency and magnitude of hydrologic disturbances to the river system are important to the development, availability, and quality of salmonid habitat upstream and in the estuary. Overbank flow contributes large woody debris that helps to structure fluvial and estuarine environments. The bulk of the sediment input to the system also occurs during high flow events. This is particularly true for the input of sand that helps to build shallow-water estuarine habitat. In the following subsections we examine historic changes in the frequency and patterns of extreme flows.

Historical Changes in Overbank Flow

The historic bankfull flow level is estimated at about 18,000 m^3s^{-1} for the mainstem Columbia River below Vancouver. This is the two-year flow recurrence level for The Dalles augmented by the typical spring-flow level for the western tributaries. Modern bankfull level is set by the standard project flood level of approximately 24,000 m^3s^{-1} for the lower river. Some overbank flow occurred in many years before 1900, in winter and in spring (Figure 28).

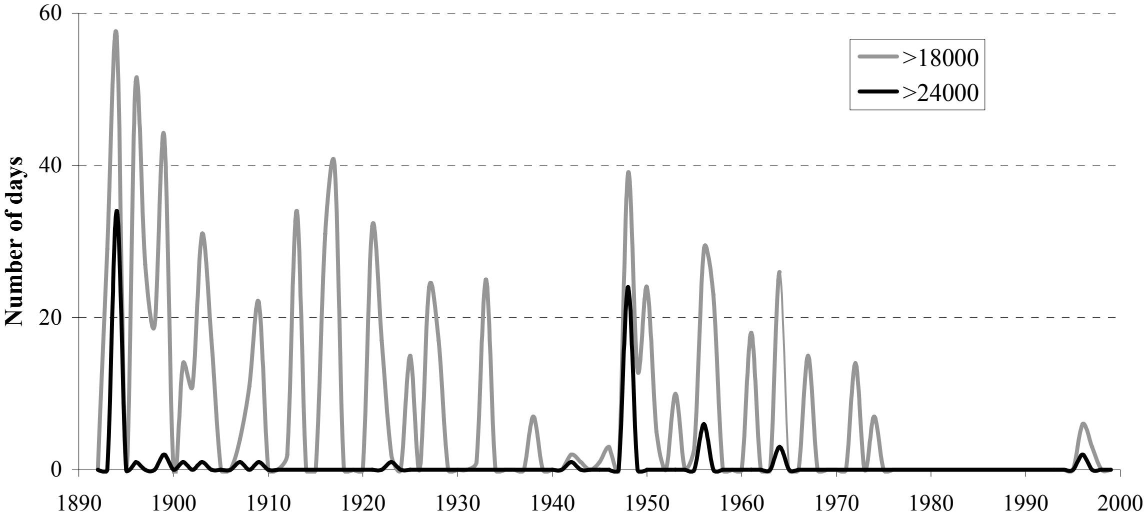


Figure 28. The incidence of flows above 18,000 m^3s^{-1} (the pre-1900 estimated bankfull flow level) and above 24,000 m^3s^{-1} (the present bankfull flow level). The present bankfull flow level has been exceeded only five times (twice in 1956) in four years since 1948. (Data adapted from USGS records.)

Substantial overbank flow (>24,000 m^3s^{-1}) is rare now, with significant events occurring only five times during the past half century—in 1948 (spring), 1956 (winter and spring), 1964–1965 (winter), and 1996 (winter). Today even historical bankfull levels of 18,000 m^3s^{-1} are rarely exceeded because of flood-control measures and irrigation depletion. The season when overbank flow is most likely also has shifted from spring to winter, because western subbasin winter floods (not eastern subbasin spring freshets) are now the major source of such flows.

Climate is a secondary factor in the incidence of overbank flow. Overbank flow events were more common during the cold PDO phase (1945–1977) than during the preceding warm PDO phase (1921–1944), even though the degree of flow regulation and irrigation depletion grew over time (Figure 29). Overbank flow is rare now even during cold PDO phases, and it was totally absent during the last PDO warm phase (1977–1995).

Changes in the River-flow Frequency Distribution

Another important symptom of human intervention in the flow cycle is the change in the frequency spectrum of the flow. There are two convenient ways to examine this spectrum:

1) the power spectrum gives a high resolution picture of the average frequency content of a process over a time period, and
2) the wavelet transformation gives a less detailed view of the time dependence of the frequency content.

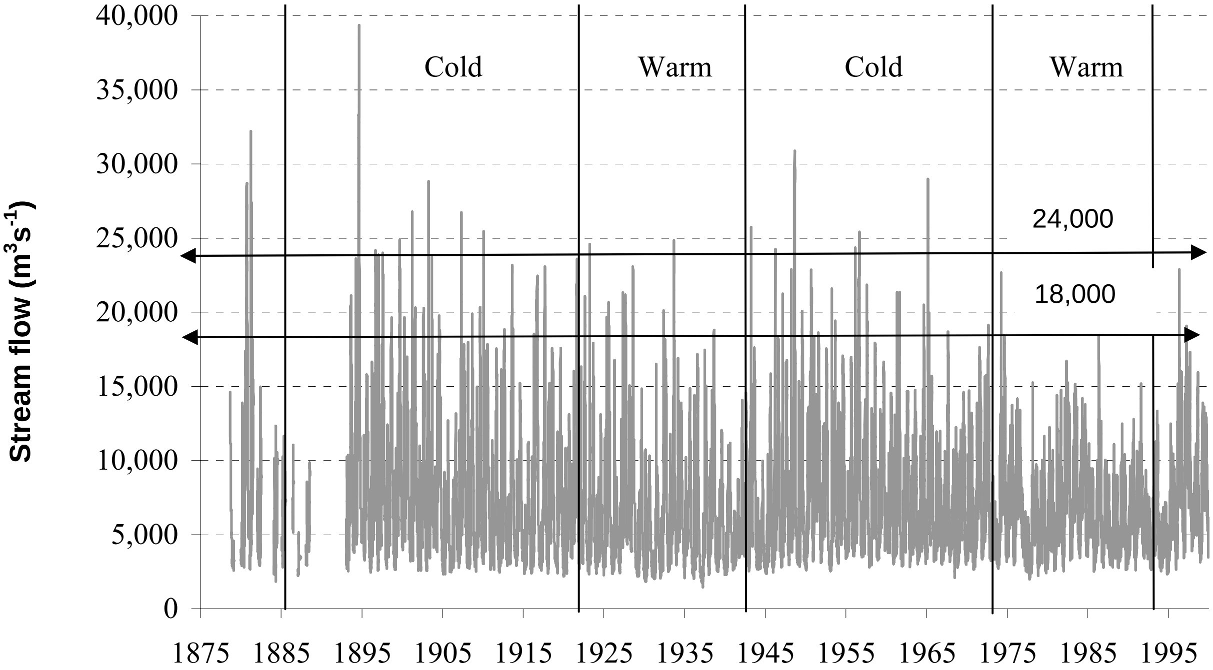


Figure 29. Monthly average flows at the Beaver Army Terminal, 1878–1999, present and historical bankfull flow levels, and warm and cold PDO cycles. Major differences between warm and cold phases of the PDO cycle in the disturbance frequency have been largely eliminated by flow regulation and diking; overbank flow is now a rare event. (Data adapted from USGS records.)

Comparison of the power spectra for the 1878–1910 and 1970–1999 periods defines the nature of the changes that have occurred (Figure 30). Low frequency flow variations with periods between about 6 and 24 months have been suppressed relative to 1878–1910 conditions; however, high frequency variations associated with power peaking have been augmented. These changes are not related to climate; the virgin-flow spectra for the two periods are similar.

The daily power-peaking cycle also perturbs the diurnal (daily) tidal signal in the river, and this effect can be seen at least as far seaward as Beaver (RKm 85). The wavelet presentation of the flow spectrum (Figure 31) shows:

1) the truncation of the annual flow cycle by flow regulation after about 1970 (despite very high virgin flows in 1972 and 1974),
2) a sharp increase in high frequency energy associated with the hydroelectric operations after about 1965, and
3) a climate (PDO cycle) influence on freshet strength (e.g., spring freshets were unusually low during 1922–1944 and higher during 1945–1976 despite flow regulation).

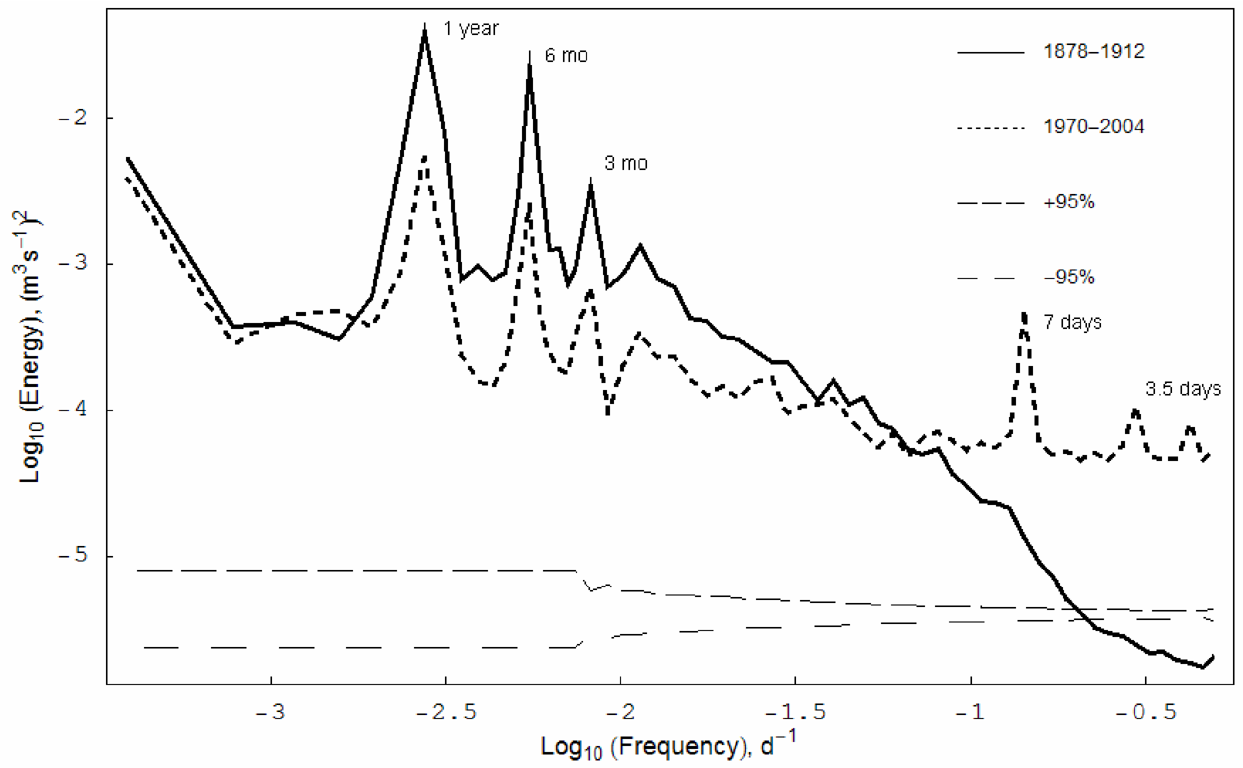


Figure 30. Power spectra of the observed daily flow at The Dalles, 1878–1910 and 1970–1999. The peaks at 1 year and 6, 4, and 3 months, which are clearly visible in the 1878–1910 record, have been greatly reduced by flow regulation and irrigation depletion. The power-peaking cycle has added energy to the system at frequencies above approximately 20 days, but especially at 7 and 3.5 days. Also shown are 95% confidence limits. (Data adapted from USGS records.)

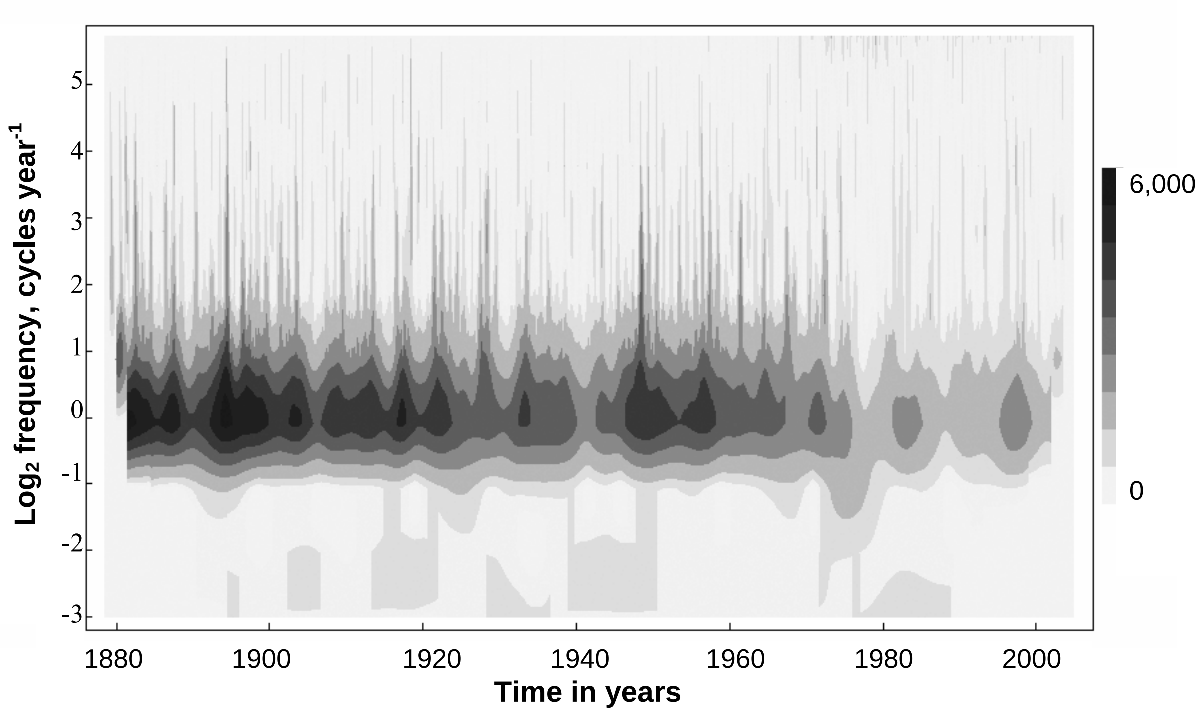


Figure 31. Scaleogram of observed flow at The Dalles. Time in years is on the x-axis, and log (base 2) of frequency in cycles per year is on the y-axis, showing periods of eight years (bottom) to 3.5 days (top). The annual cycle is denoted by $\log_2$ (frequency) = 0 (1 cycle year^{-1} or $2^0 = 1$), and a period of six months by $\log_2$ (frequency) = 1 (2 cycles year^{-1} or $2^1 = 2$) (modified from USGS). The annual cycle becomes markedly weaker after approximately 1970 (as indicated by the loss of black and dark gray areas after 1970), primarily due to flow regulation. Climate variations such as the PDO cycle also affect the annual cycle. Also after 1970, high frequency (weekly) flow variations are much more prominent (note gray lines at top right), due to power peaking. (Flow data adapted from USGS records.)

Climate and Human Influences on Freshet Styles

Although the flow cycle is different each year, certain frequently occurring types of flow events or freshet styles are apparent. These patterns strongly affect flow and sediment transport processes in tributaries and the mainstem Columbia River, and they are sensitive to human and climatic change. Three principal kinds of spring freshets are evident, distinguished by the source of flow:

1. Large winter snowpack without exceptional spring rain (e.g., 1880, 1916, 1972, 1974, and 1997). Very late spring freshets are likely to be in this category.
2. A normal winter snowpack followed by a very wet spring. The result is heavy snow in April and early May and then very heavy spring rains that rapidly melt an unconsolidated snowpack (e.g., 1948).

3. A large winter snowpack and heavy rains. The only certain example of this is 1895 (USGS 1949), although some of the other very high spring freshets of the 19th century were likely of this sort (e.g., 1849, the second-highest known freshet, intermediate between 1948 and 1894).

Heavy spring rains in 1894 and 1948 accelerated the spring freshet so that the maximum flow was not unusually late, even though a cold spring had allowed the low elevation snowpack to grow until the onset of the freshet. Winter freshets caused by rapid snowmelt and thawing of poorly vegetated eastern subbasin soils are known to cause unusually large sediment transport, especially for fines (Haushild et al. 1966, Waananen et al. 1971). Sediment-transport data collected during 1963–1964 by the USGS suggest that the Snake River basin also contributes considerable fine sediment during spring in some years. The U.S. Army Corps of Engineers (USACE) indicates that 75–110 × 10^6 m^3 (roughly 150–220 10^6 mt) of sediment have accumulated behind the four Snake River dams built since these measurements were conducted, considerably reducing the supply of sediment to the mainstem Columbia.

Most major winter freshets in the Columbia Basin are the result of rain-on-snow events that cause rapid melting of a low elevation snowpack. Four types of winter freshets can be defined based on the importance and location of the low elevation snowpack that is melted:

1) primarily western subbasin, with snowmelt (e.g., 1894 and 1997),
2) eastern and western subbasin, with snowmelt (e.g., 1861, 1881, and 1996),
3) primarily eastern subbasin, with snowmelt (e.g., December 1933, although the Cowlitz and some coastal rivers also flooded), and
4) primarily western subbasin, with little snowmelt (e.g., January 1923, although 1909 and 1927 had similar storms).

The first three of these freshet types require that a low elevation snowpack be melted by a "Pineapple Express" storm, a weather pattern from the south carrying warm temperatures. If no low elevation snowpack exists, a major winter freshet rarely occurs. Exceptional rainfall for several weeks, however, did lead to a flood in January 1923 although the low elevation snowpack had melted before the main flood peak (Brands 1947).

Winter freshets are spatially more diverse than spring freshets, because winter freshets are primarily a response to a specific storm or series of storms, with attendant large spatial variability. The 1933–1934 winter storms affected the Wenatchee River in Washington and tributaries very strongly. Flows in 1881 were very high in the Willamette and Umatilla rivers in Oregon. The Canadian part of the basin usually plays only a minimal role in winter freshets, because high temperatures do not penetrate to this part of the basin during most storms.

While total winter snowpack differs among subbasins, spring freshets are more similar from year to year, because they represent an average over the entire winter of storm intensity. Winter freshets are, as noted previously, a very potent source of sediment. Flow regulation is most effective in controlling freshets related solely to the spring melting of a large winter snowpack, because a planned prerelease of water can begin in December or January, 5–6 months before the onset of the freshet. It is more difficult to anticipate or predict the occurrence of heavy spring rains, and little preparation can be expected for such events. Winter freshets also are difficult to control, especially when they originate largely in the western subbasin, where precipitation rates are higher and storage capacity relatively low. Flow from rain-on-snow events, whether in the winter or the spring, is more difficult to control than the normal spring snowmelt, because the melt rate is higher.

Warming of the climate over the past century and flood control appears to have reduced the intensity of flow resulting from winter rain-on-snow events in the western subbasin. There were four large 19th century Willamette River floods (1813, 1861, 1881, and 1890) but only two major events during the 20th century (1964 and 1996); flows in 1813 and 1861 appear to have been larger than in any 20th century winter event, and maximum flow during the freshet of 1996 was only approximately 53% of that estimated for 1861, the largest known event. Newspaper accounts from the 19th century indicate that more than 1 m of snow sometimes accumulated on the ground in the Willamette Valley, a rare event since 1900. The incidence of winter freshets that affected the western and eastern subbasins, however, may have increased during the past century.

Spring freshets related to heavy spring rains are uncommon, and it is not known whether their incidence has changed.

Downstream Effects of Hydrological Alterations

Salinity Intrusion and Salinity Stratification

Salinity intrusion length and density stratification because of vertical salinity gradients have likely increased over the past century. Salinity intrusion is governed by three primary factors:

1) channel controlling depth,
2) the strength of the tides, and
3) river flow.

The dependence of salinity intrusion on the channel controlling depth (H) is very strong. The landward, near-bed mean flow that drives salinity intrusion varies with the H^2 or H^3, and the dependence of salinity stratification is even stronger, H^4 or H^5. The tides have a complex effect on salinity. Tide-induced vertical turbulent mixing inhibits salinity intrusion, while horizontal transport by the tides is the primary salt transport mechanism during periods of strong tides and low-to-moderate river flows.

Salinity stratification increases with river flow, whereas the relationship between salinity intrusion length (L_S) and river flow (Q_R) is inverse $L_S \approx Q_R^{-n}$. Values of n vary from system to system from about 0.5 to greater than 1; the value for the Columbia River is not known. While this might suggest that the river-flow influence is smaller than other factors, river flow may vary seasonally by an order of magnitude.

Before flows were regulated, the possible range of observed flow variation was even larger than at present, ranging from 1,000 to 35,000 m^3s^{-1} at The Dalles. In contrast the tidal range varies by only a factor of about two over the neap-spring cycle. The tidal prism has been reduced by about 15% by diking and filling, and the controlling channel depth has doubled over the past 120 years. Changes in bathymetry probably have caused the largest changes in salinity intrusion and density stratification (Figure 32), but reduction of the spring freshet also has increased salinity intrusion and salinity stratification.

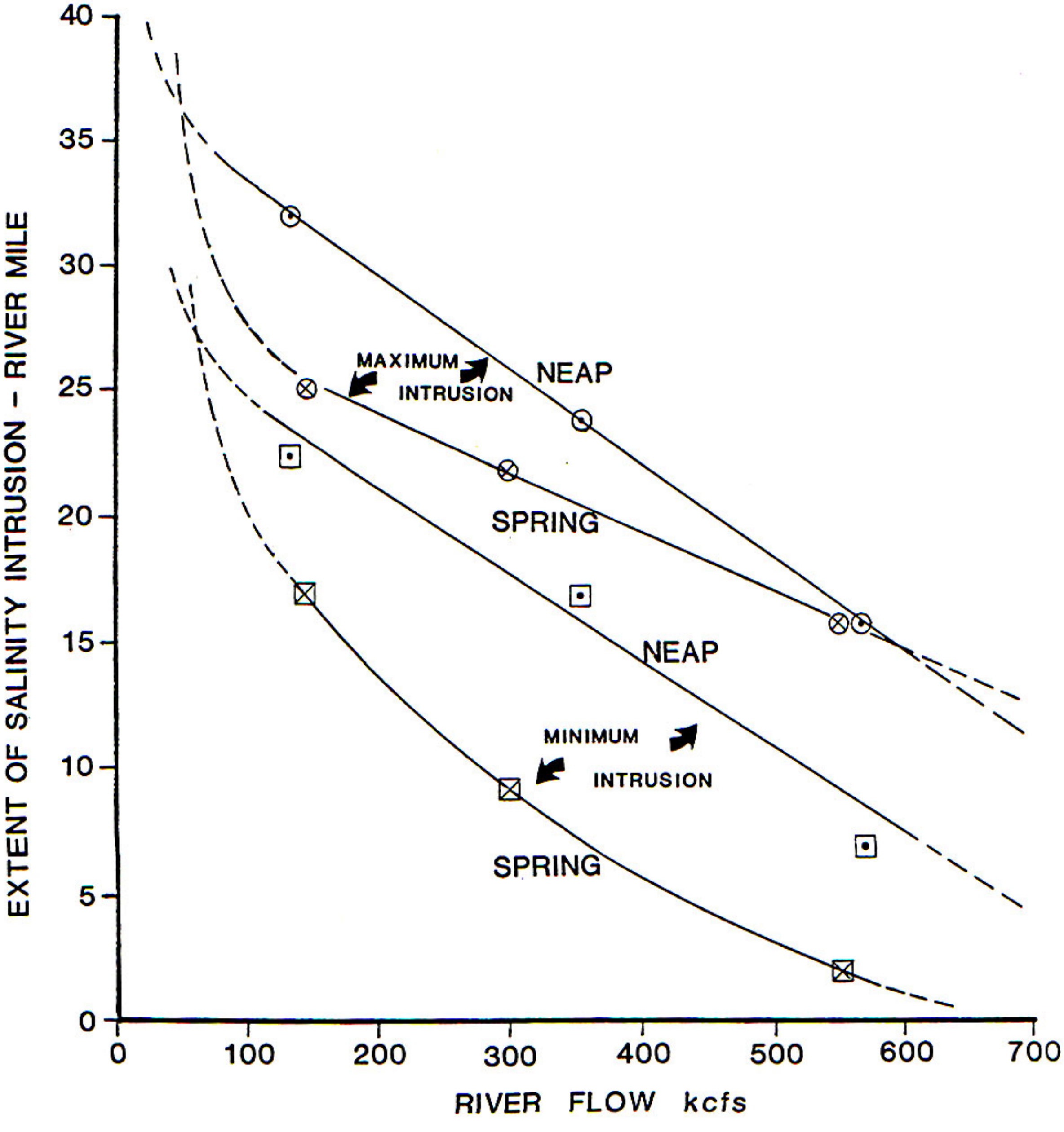


Figure 32. Maximum (end of flood) and minimum (end of ebb) salinity intrusion distance in the Columbia River estuary, based on 1980 bathymetric conditions. Present salinity intrusion may be somewhat different because of deepening of the navigation channel at the entrance. (Reprinted with permission from Jay 1984.)

Tidal Regime and River Stage

River flow and tidal propagation interact strongly (Jay and Flinchem 1999, Kukulka and Jay 2003a). The major daily and twice-daily tidal components (the major tidal species) are damped by river flow Q_R; tidal amplitudes and tidal range vary according to Q_R^n, n is between negative 0.1 to negative 0.5. The distortion of the tide that determines the timing of high and low waters is more strongly affected. Daily and weekly power peaking by the hydropower system further complicates river tides by adding pseudotides that propagate seaward from Bonneville Dam (rather than landward from the ocean). Pseudotides can be larger than the natural tide landward of Portland. Changes in the seasonal flow cycle have increased tides and tidal currents in the spring and early summer and damped them in the fall and winter. Dredging also may have influenced tidal propagation in the tidal-fluvial reach, contributing to approximately an 8% increase in tidal amplitudes over the past century.

While little is known about the direct impacts on juvenile salmonids because of increased tidal fluctuations and currents during the spring season, substantial changes in the availability of shallow-water habitat area (SWHA) have occurred.

Shallow-water Habitat Availability

River stage (the water level averaged to remove tidal variations) increases rapidly with river flow. Reduction of maximum flow levels, dredged material disposal, and diking/flood protection measures have essentially eliminated overbank flow (Figure 28 and Figure 29) in the estuary and the tidal-fluvial part of the system below Bonneville Dam. The greatest reductions in river stage have occurred during the spring-freshet season, when juvenile salmonid densities are high. Kukulka and Jay (2003b) investigated the changes in SWHA (including SWHA in the former floodplain) for a sample reach extending from Skamokawa, Washington, to Beaver (RKm 50–RKm 85) during the 1974–1998 period. They defined SWHA as areas with water depths between 0.1 and 2 m for any given river stage.

Four scenarios were considered:

1) the natural state (virgin flow, no dikes),
2) present conditions (observed flow with dikes),
3) virgin flow with dikes, and
4) observed flow without dikes.

Analysis of these scenarios allows evaluation of the impacts of diking and flow regulation, separately and together.

During the spring-freshet season (May–July), dikes and flow alteration combined reduced average SWHA in the study reach by 62%, from 4.5 to 1.7×10^7 m^2. Taken individually, diking would have reduced average freshet-season SWHA by 52%, from 4.5 to 2.2×10^7 m^2; flow-cycle alteration would have reduced SWHA by 29%, from 4.5 to 3.2×10^7 m^2. Not only has habitat been lost, but the remaining SWHA is at a lower elevation than was historically the case because of the reduction of river stage during the spring season. The remaining SWHA also experiences stronger tides than occurred historically. That the total reduction (62%) is less than the sum of individual reductions from flow regulation (29%) and diking (52%) indicates that the flood-protection engineering for the system is redundant, a common engineering strategy. This redundancy implies that any habitat restoration in this reach will probably require some balance between flow restoration and dike removal.

Kukulka and Jay (2003b) found that higher river stages greatly increase SWHA over a 40 RKm stretch, but numerical modeling results (see the “Estuarine Habitat Opportunity” section, page 89) do not show such a clear pattern. This difference is explained by the inclusion of the entire floodplain (including the dike portion) in the Kukulka and Jay model; model results (see the “Estuarine Habitat Opportunity” section, page 89) do not include diked areas. This contrast emphasizes the historical importance of the prediked floodplain in providing shallow habitat.

Estuarine Sediment Dynamics

The estuary and its food web can be affected by sediment inputs in a variety of ways:

1. Continual sediment supply is needed to counter erosion of marshes and sea-level rise (≈1 mm per year in the estuary). The effects of changes in quantities and types of sediment input on estuarine wetlands have not been investigated.
2. The organic component of the sediment supply is a vital source of nutrition to the food web of the ETM (Sherwood et al. 1990, Simenstad et al. 1990a and 1992), which is based on microbial processing of fluvial organic detritus. Much of this organic matter now stems from phytoplankton production in the reservoirs, whereas it previously contained a much higher percentage of material from floodplain inundation and estuarine marshes. These changes may have affected the food supply for juvenile salmonids, but the changes have not been quantified.
3. Decreased turbidity during the freshet season may increase vulnerability of salmon to avian predators. This could be an important factor in light of the increased numbers of predators that have become established on artificial sand islands in the estuary (see the “Estuarine Habitat Capacity” section, page 127).
4. The reduction in sediment transport to the estuary has affected navigation by reducing the amount of sand that must be dredged from estuarine channels.

The ecological responses to changes in sedimentary regime have been poorly investigated. Understanding the effects on juvenile salmonids will require physical/chemical, geological, and biological observations, and perhaps numerical sediment-transport modeling.

Effects of Future Climate Change

Human intervention in the flow cycle has had a bigger effect on Columbia River hydrology than climate variations during the past 140 years. The projected near-term effects of climate are not large enough to rival the impacts of human alterations to the flow cycle. Future climate change, however, may exacerbate conflicts over water supply by increasing demand and decreasing natural flows during the critical spring-freshet period (Hamlet and Lettenmaier 1999). To the extent that future climatic changes alter the spatial and temporal patterns of flow across the basin, influences on local salmon populations and life histories could be significant.

Changes in the PDO could have an important impact on future patterns of flow and sediment flow in the Columbia River basin. While it was widely believed that the PDO cycle changed back to a cold phase in the late 1990s, these conditions did not persist and have given way to warm coastal temperatures off Oregon since 2002. It remains unclear whether global warming will affect the characteristic interdecadal cycling of warm and cold phases observed in the past.

An important factor in the PDO cycle is its synergy with ENSO cycles. La Niña winters during the cold PDO phase tend to be unusually severe (e.g., 1997 and 1999), while the effects of El Niño are muted. It is possible, however, that global warming could alter the duration of cold and warm phases or the relationship between the PDO and ENSO cycles.

Climate projections predict gradual regional warming, possibly accompanied by higher precipitation, especially in winter (Hamlet and Lettenmaier 1999). Just as the ratio of winter to spring flows is naturally higher than in the Fraser River because of the Columbia River's more southerly position, a warmer climate will likely increase Columbia River flows in winter and decrease peak and average spring-freshet flows. Of the three spring-freshet styles, flow regulation and diversion already have decreased flow volumes associated with the two that depend on an exceptional winter snowpack. Climate change probably will decrease (and already may have decreased) the probability of a 1948-style freshet caused by heavy spring precipitation on a late-arriving snowpack, because increased temperatures may not allow significant snow accumulation in April and early May.

Effects of global warming also may vary among Columbia River subbasins. The frequency of major winter freshets (rain-on-snow events) in the eastern subbasin probably will increase unless the warming is sufficient to eliminate the low elevation snowpack. This probably will increase the supply of fine sediment to the river and estuary. Winter freshets in the western subbasin that do not involve snowmelt might increase in frequency or severity. However, low elevation snow accumulation west of the Cascades probably will decrease, reducing the frequency of major western subbasin freshets from rapid snowmelt even if rainfall increases. The net effects of such change on sediment supply in the western subbasin are unclear.

Implications of Hydrological Change for the Member/Vagrant Hypothesis

The member/vagrant hypothesis (Sinclair 1988, see the "Conceptual Framework for Evaluating Estuarine Habitat Conditions" section, page 21) predicts that diverse salmon life histories have developed in response to certain persistent features of the physical environment. Thus alternative salmon rearing and migration behaviors become linked to various habitats and environmental conditions capable of supporting each developmental stage (e.g., egg, fry, smolt, etc.) within a suitable range of times and locations for individuals to complete their life cycles. If this is an accurate depiction of salmon life histories, then major departures from the historical template of an ecosystem may create mismatches between established salmon behaviors and the physical environment or prevent the expression of potential behaviors by eliminating habitat opportunities (Figure 9). The hydrological changes, particularly those associated with flow regulation, water withdrawals, floodplain diking, and habitat loss, represent a fundamental shift in the physical state of the entire Columbia River ecosystem. Such changes have significant consequences for salmonids whose migration and rearing behaviors have adapted to historical conditions for the estuary and, therefore, for each of the components of salmon performance defined by our conceptual framework (Figure 33).

For example, the effort to stabilize flows in the Columbia River basin ironically may create less stable patterns for salmonids whose migration and rearing behaviors have adapted to historical patterns of hydrologic variability. The reduction of the spring freshet to which the timing of downstream migrations and patterns of habitat use of some subyearling and yearling life history types may have been linked is particularly important. By creating selective advantage for those behaviors that match the operations of bypass, spill, and transportation systems, life history variation among salmonids may be simplified to conform to narrow

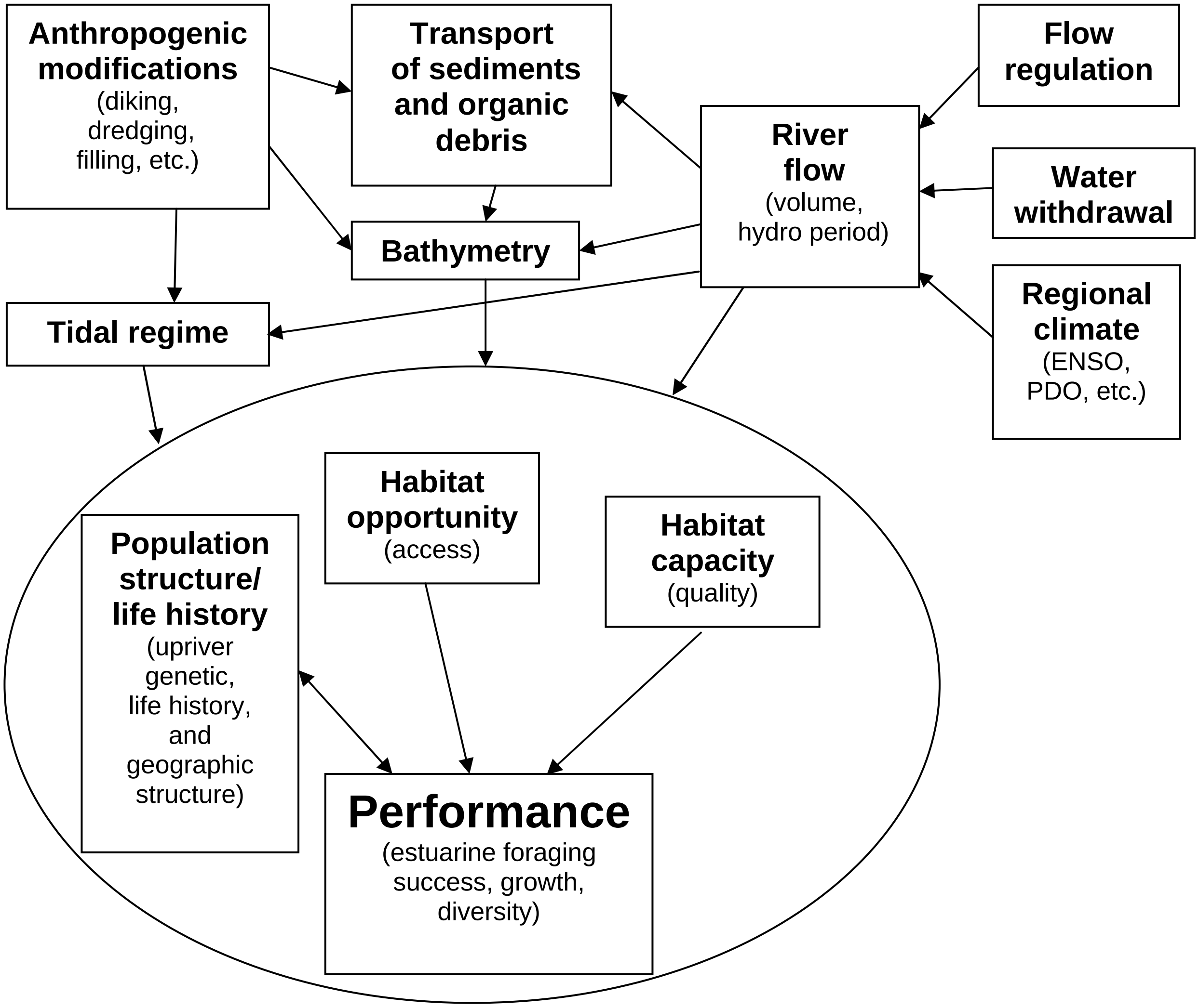


Figure 33. External factors affecting disturbance processes and the physical template of the estuary.

windows of opportunity now prescribed by the management system (ISG 2000, Williams in press). One potential result of dampening flow variations in the Columbia River could be a greater uniformity of migration patterns with potential consequences for the variety of times and sizes at which salmon arrive in the estuary or ocean or both.

The nearly complete elimination of overbank flooding throughout the expansive tidal freshwater portion of the estuary may pose some of the most significant consequences for Columbia River salmonids. Flow regulation and diking effects have largely eliminated access to off-channel floodplain habitats and refugia during high flow events. If, as we suspect, patterns of extended estuary use by small subyearling migrants are directly linked to the availability of shallow-water habitat, then loss of the tidal floodplain may simplify salmon diversity. In the "Estuarine Habitat Opportunity" section (page 89), we evaluate use of a hydrodynamic model to better understand the habitat-opportunity dynamics and the implications for estuarine-rearing salmonids.

In addition to the physical effects of reduced habitat opportunity on salmon diversity, flow regulation and diking may influence the productive capacity of the estuary by regulating energetics processes (e.g., habitat capacity), including food production, competition, and predation. Floodplain inundation greatly increases the surface area of tidal estuarine and riverine habitats available to salmonids. This allows fish to expand their distribution into productive off-channel areas and may relax competitive interactions by reducing fish densities. Studies on a nontidal portion of the lower Sacramento River in California found that tagged juvenile Chinook salmon released in the seasonally inundated floodplain had better growth, higher consumption rates, and improved survival compared to others released into the main river channel (Sommer et al. 2001). Elimination of overbank flooding also prevents the pulsed delivery of structural and energetic components to the rest of the estuary (e.g., large wood pieces, sediments, detritus, and prey organisms produced in adjacent riparian and floodplain habitats). In the "Estuarine Habitat Capacity" section (page 127), we will examine what is known about changes in habitat capacity of the Columbia River estuary.

Conclusions

Human and Climate Influences on Flow and Sediment Transport

Columbia River mainstem flow and sediment transport affect salmonids directly and indirectly. Major changes during the past 120 years in Columbia River hydrological processes have resulted primarily from human alteration to the system and secondarily from climate processes.

Large-scale Geography

The Columbia River has the largest flow ($\approx$7,300 m^3s^{-1}) of any river on the Pacific coast of North America. Its annual average sediment transport ($\approx 10^7$ mt year^{-1}) is not unusually large, and is exceeded by several other western rivers. For hydrological purposes, the Columbia River basin can be divided into western and eastern subbasins by the Cascade Mountains. Except for the Canadian portion, the eastern subbasin (with 92% of the surface area and 75% of the flow) is relatively arid. Almost all flows from the eastern subbasin pass the gauge at The Dalles, which has the longest daily flow record on the West Coast (1878–present). The western subbasin contains only 8% of the area of the entire Columbia River basin, but it contributes about 25% of the flow. The Willamette River is typical of the western subbasin; the flow record at Albany extends from 1892 to the present.

Climate Change

Climate and flow conditions during the last half of the 19th century reflected the end of the Little Ice Age from about 1400 to 1850. This period was significantly cooler and wetter than present conditions. For example, 10 of the 14 strongest known spring freshets in the system occurred between 1849 and 1900, even after accounting for human manipulation of the flow.

Climate Cycles

Cyclical climate phenomena exert a strong influence on Columbia River hydrology. Although the history of regional climate fluctuations during the 19th century is unclear, effects of two cyclical processes were prominent throughout the 20th century:

1. The PDO has a cycle that lasts 40–60 years and probably has been active for at least 300 years. Cold PDO phases (e.g., 1945–1976) are generally associated with high river flows and are favorable for salmonid production in the Pacific Northwest; warm phases (e.g., 1977–1995) are characterized by low river flows and are less favorable for salmonid production.
2. Indices of the ENSO (typically 3–7 years in duration) also are correlated with Columbia River flow. ENSO cycles affect survival of salmonids in the fluvial, estuarine, and ocean environments.

Pacific Decadal/El Niño Southern Oscillation Interaction

The PDO and ENSO cycles interact such that El Niño years are most intense during the warm PDO phase and La Niña years during the cold PDO phase. The average annual Columbia River flow at The Dalles is 111% of normal during cold PDO/La Niña years, whereas it is only 85% during warm PDO/El Niño years. The corresponding figures for the Willamette River are 119% and 81%.

Latitudinal Position

The Columbia Basin's climate response is conditioned by its position within a latitudinal band of strong response to the ENSO and PDO cycles. The flow-per-unit area is greater in the western than in the eastern subbasin, and latitudinal differences in the timing of snowmelt influence spring-freshet properties. Still variations across the basin in response to ENSO or PDO forcing are modest.

Climate Effects on Sediment

Flow fluctuations are amplified by fluvial sediment transport, because sediment transport varies more than linearly with flow. Total sediment load during cold PDO/La Niña years is more than 200% of that during warm PDO/El Niño years in the Columbia (at Vancouver) and the Willamette rivers. Climate effects on sand transport are even stronger than those on total load.

Annual Average Flow at The Dalles

Changes in annual average flow are an important integral measure of system alteration. The mean annual average flow of the Columbia River at The Dalles has decreased about 16.9% from 6,320 m^3s^{-1} (1879–1899 estimated natural or virgin flow) to 5,250 m^3s^{-1} (1970–1999 observed flow). We estimate that climate change accounts for an 8–9% decrease, deforestation a 1–2% increase, and irrigation depletion approximately a 7.4% decrease in average annual flow.

Spring-freshet Properties

Spring-freshet timing, strength, and duration are important to downstream migrant juvenile salmon. Spring-freshet properties have been much more highly altered than the mean flow. The average natural or virgin flow for the spring-freshet season (May–July) was approximately 13,600 m^3s^{-1} before 1900. This has decreased by approximately 5,870 m^3s^{-1} (43%) to 7,740 m^3s^{-1}, with 26.5% because of flow regulation, 11% because of irrigation depletion, and 5.6% because of climate change. Thus freshet-season flow at The Dalles is now only 148% of the present (reduced) mean flow, while it was 215% of the higher 19th century flow. Flow regulation and the annual irrigation cycle also have increased fall and winter flows, the latter because of water released before the freshet.

Maximum Daily Flow at The Dalles

The observed maximum daily spring-freshet flow has been reduced slightly more than freshet-season flow, from 19,300 m^3s^{-1} (1858–1999) to 10,870 m^3s^{-1} (1970–1999), a decrease of 44%. This is a drop from 305% to 207% of the mean flow.

Spring-freshet Timing at The Dalles

The timing of the maximum spring-freshet flow also changed. Maximum daily spring-freshet flow now typically occurs at about water-year Day 242 (May 29), whereas maximum flow occurred in the 19th century at about water-year Day 256 (June 12), a shift of two weeks.

Willamette River Hydrology

Changes in the western subbasin have been similar to those in the eastern subbasin, but the changes are not as well documented. The observed annual average Willamette River flow at Albany has decreased from 462 m^3s^{-1} for 1893–1900 to 394 m^3s^{-1} for 1970–1999, or 14.8%. Late summer and fall (August–December) flows have been augmented; whereas, average monthly flows during the January to July period have decreased.

Columbia River Flow at the Mouth

The long-term average flow at the mouth of the Columbia River was 7,300 m^3s^{-1} for 1892–1999. The Columbia River flow at the mouth prior to 1900 was approximately 8,530 m^3s^{-1} and has decreased to approximately 7,080 m^3s^{-1} for 1970–1999 (≈17%).

Changes in Sediment Transport

Sediment transport is a vital system characteristic for salmonids. Hindcasts from limited data collected during the 1960s suggest that the annual average sediment transport from the eastern subbasin decreased from about 21 × 10^6 mt for 1858–1878 to approximately 8 × 10^6 mt for 1970–1999, (≈60%). We estimate that historical sand transport of more than 10 × 10^6 mt for 1858–1899 decreased to 3.2 × 10^6 mt (≈70%). Most of the reduction in eastern subbasin sediment transport is related to the dam system, especially its reduction of spring-freshet flow. In the Willamette River, historical sediment transport for 1893–1903 was approximately 2.4 × 10^6 mt, compared to only 1.5 × 10^6 mt for 1970–1999, a reduction of approximately 35%.

Disturbance Frequency

The frequency and magnitude of disturbance to the river system is important to salmonids. The historical bankfull flow level was approximately 18,000 m^3s^{-1} for the main stem below Vancouver. Modern bankfull level is set by the standard project flood level of approximately 24,000 m^3s^{-1} for the lower river. Some overbank flow occurred in many years before 1900. Flow regulation and water withdrawal have made overbank flow (above 24,000 m^3s^{-1}) rare, with significant events occurring only five times since 1948. Climate is a secondary factor with regard to the incidence of overbank flow. Overbank flow is now rare even during cold PDO phases, and it was totally absent during the last PDO warm phase (1977–1995).

Changes in Shallow-water Habitat Area

Hindcasts based on topography and simple tidal models suggest that, during the spring-freshet season (May–July), dikes and flow alteration combined have reduced average SWHA in the Skamokawa to Beaver reach by 62%, from 4.5 to 1.7 × 10^7 m^2. Individually, diking would have reduced average freshet-season SWHA by 52% (from 4.5 to 2.2 × 10^7 m^2); flow-cycle alteration alone would have reduced SWHA by 29% (from 4.5 to 3.2 × 10^7 m^2). Not only has habitat been lost, but the remaining SWHA is at a lower elevation than it was historically because of the reduction of river stage during the spring season. The remaining SWHA also experiences stronger tides relative to those of the historic period.

Changes in the River-flow Frequency Distribution

Low frequency flow variations with periods between about 2 years and 6 months have been suppressed by the dam system, whereas high frequency variations associated with power peaking have been augmented. The daily power-peaking cycle also perturbs the diurnal (daily) tidal signal in the river.

Spring-freshet Styles

The flow cycle is different each year, but three patterns of spring freshets commonly occur:

1) large winter snowpack without exceptional spring rain,
2) normal winter snowpack with very high spring rainfall, and

3) large winter snowpack combined with very high spring rainfall.

The largest known freshet (1894) was Type 3, and the second largest (1948) was Type 2.

Winter-freshet Styles

Four types of winter freshets are evident, based on the source of the flow:

1) western subbasin only, with extensive snowmelt,
2) eastern plus western subbasin,
3) eastern subbasin only, and
4) western subbasin only, without extensive snowmelt.

The first three types of winter freshets are generated by rain-on-snow events, and the largest known freshets (e.g., 1861, 1881, and 1892) involved both subbasins. The Canadian portion of the eastern subbasin is not usually affected by these floods.

Downstream Effects of Hydrological Alterations

Changes in Columbia River flow and sediment transport have exerted an important influence on the estuary, but these changes are not well understood. Effects of these hydrological changes on the Columbia River buoyant plume in the coastal ocean are almost unknown. The following downstream effects of hydrological change should be considered by future studies:

- estuarine salinity intrusion and salinity stratification,
- habitat availability,
- the fluvial tidal regime,
- sediment dynamics, and
- Columbia River plume area, volume, turbidity, and seasonality.

Effects of Future Climate Change

Although climate effects on hydrology have been and probably will remain smaller than those of human manipulation, it is still vital to consider how climate will constrain future management options in the Columbia Basin, including efforts to restore depleted salmon populations. Climate projections suggest gradual regional warming, possibly accompanied by higher precipitation, especially in winter. This would likely lead to increased incidence of winter freshets and lower natural spring-freshet flows.

These changes would likely exacerbate conflicts over water supply during the critical spring-freshet period, by increasing demand and decreasing natural flows.

Implications for Salmon Diversity and Productivity

Dampening of established flow variations in the Columbia River estuary through flow regulation may have important impacts on salmon diversity and productivity. Simplification of flow patterns may reduce the diversity of salmon migration patterns with potential effects on arrival times and sizes of fish entering the estuary and ocean. Reduced floodplain inundation has eliminated shallow-water habitats, which probably were seasonally important rearing areas and refugia for juvenile salmon, particularly for small subyearling migrants. Disconnecting the tidal river from its floodplain also prevents delivery of wood debris, organic matter, and prey resources to the estuary, with potential consequences for estuarine food chains.

Estuarine Habitat Opportunity

Introduction

Dynamics of Habitat Opportunity

In the previous section, we reviewed changes in regional climate and basin-wide hydrology that define the past and present range of physical conditions for salmon upstream and within the Columbia River estuary (see the “Changes in Hydrological Conditions” section, page 47). In this section,[4] we shift our perspective to the internal dynamics of physical change within the estuary. We examine the effects of changing river flows and estuarine bathymetry on one of the principal attributes of salmon performance as defined by the member/vagrant hypothesis (see the “Conceptual Framework for Evaluating Estuarine Conditions,” section, page 21)—habitat opportunity (Figure 34).

Estuarine habitat opportunity for salmon is naturally dynamic, because physical characteristics of the estuary (e.g., water depths, current velocities and directions, salinities, and temperatures) continually change with tides and river flow. Young salmon in the estuary may constantly need to adjust their distributions and behaviors to a shifting habitat landscape. Accessibility of some estuarine habitats depends on two factors:

1) the frequency of tidal or seasonal inundation, or
2) whether changes in physical or chemical conditions at a particular site remain within a suitable range of physiological or ecological tolerance among individuals.

For example, many productive shallow-water habitats that subyearling salmon use for extended periods of estuarine rearing drain at low tide and are only accessible for a limited number of hours during each tidal cycle (Levy and Northcote 1982, Healey 1982).

In this section, we evaluate a simulation model as a tool for understanding the habitat-opportunity dynamics for salmon and the potential effects of anthropogenic changes in the estuary that affect these dynamics. We begin by describing our modeling approach and the physical indicators we have chosen to define habitat opportunity for subyearling salmon. We then use the model to assess the behavior of these criteria under present and historic river-flow and bathymetric conditions. We also review these model results and their implications for the member/vagrant hypothesis.

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[4] Since the time of research described in this section (1998–2000), the methodology has been substantially extended through the development of three-dimensional baroclinic circulation models and simulation databases for the Columbia River (Zang et al. 2004, Baptista et al. 2005) and by the modification of criteria for habitat opportunity to account for three-dimentional information on velocities and for information on salinity (USACE 2001) and temperature. While the results herein no longer reflect state-of-the-art modeling capabilities, the section correctly depicts the concepts underlying the methodology and their application to the dynamics of salmon habitat opportunity.

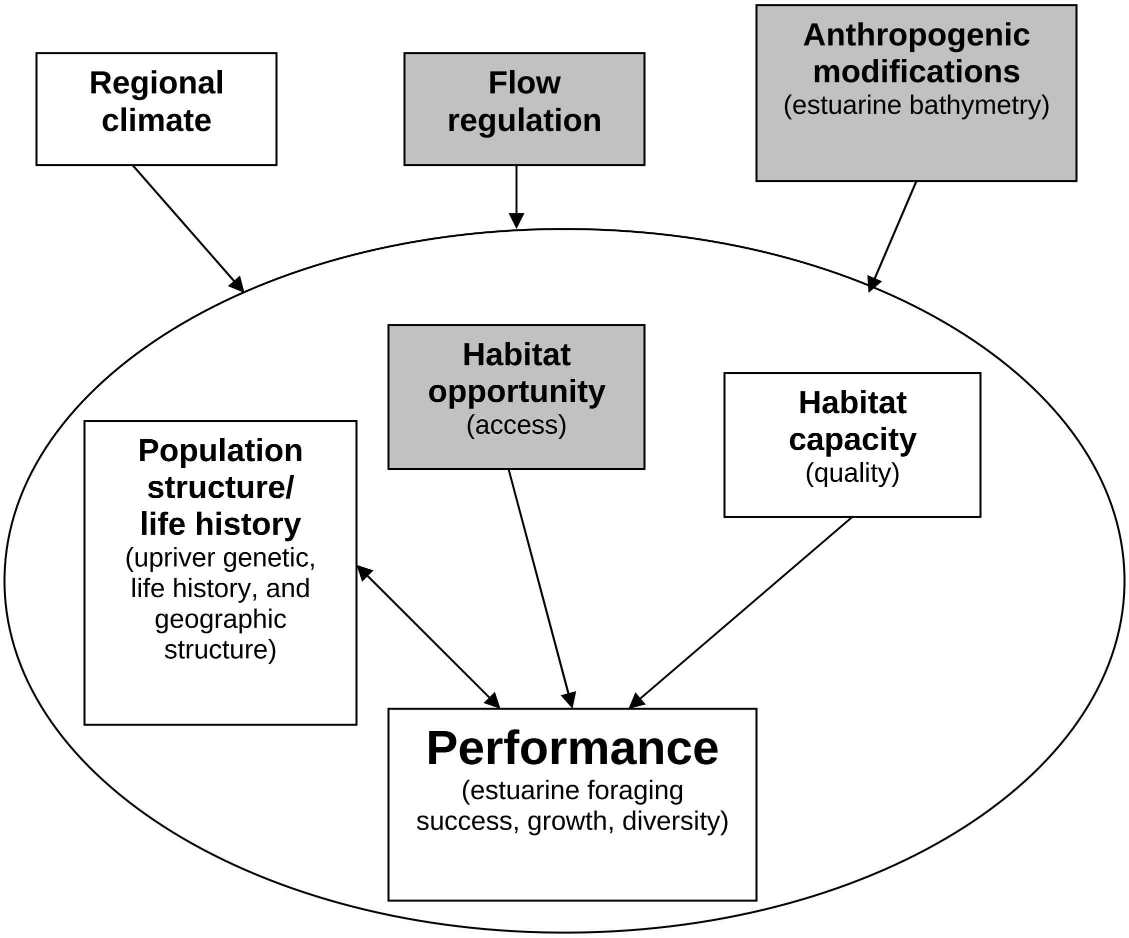


Figure 34. Physical modifications to the estuary affect habitat opportunity for salmon. This chapter uses simulation modeling to examine effects of flow regulation and bathymetric change.

Modeling Approach

The Center for Coastal and Land-Margin Research (CCALMR) has been developing an observation and forecasting system for the Columbia River estuary since 1996 (OGI 1997, Baptista et al. 1999). The Columbia River Estuary Forecasting System (CORIE), a multipurpose infrastructure system for science and management, includes integrated modeling and observation components that regularly generate a variety of products describing the physical environment of the Columbia River below Bonneville Dam (RKm 235).

Daily forecasts of depth-averaged circulation made since 1997 are among the regular CORIE products (OGI 1997). At the core of the forecasts is a numerical model, which solves for mass and momentum conservation equations inside a predefined computational domain, given bathymetric and boundary forcings. Circulation is described in the form of water levels and velocities, in a computational grid that extends from Longview, Washington (RKm 105), to the Pacific Ocean (Figure 35). Circulation forecasts are generated daily, with predictions compared against real-time observations from the CORIE network (Baptisa et al. 1998 and 1999). This

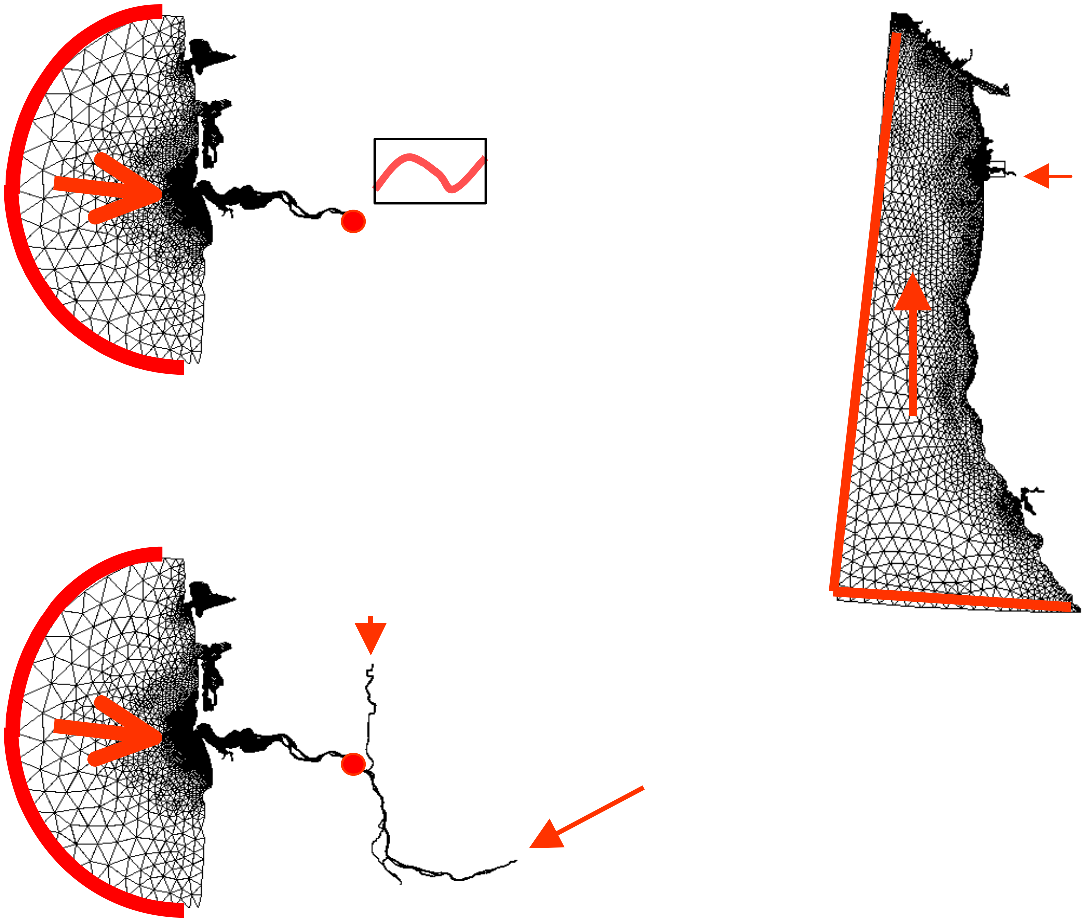


Figure 35. Different domains of simulation within CORIE. The domain for depth-averaged hindcasts (bottom left) conducted 1997–2001 is the basis for the simulations in this technical memorandum. It extends from the Bonneville Dam, the Willamette Falls in the Willamette River, and the upstream Cowlitz River into the continental shelf. Tides are applied at the ocean boundary (bold line). Wind forcing is applied at the ocean (big arrow). The small arrows represent river discharges applied as boundary conditions. The Beaver Army Terminal (dot) is no longer a boundary condition. The domain for depth-averaged forecasts (top left) conducted 1997–2001 extends from Beaver into a limited portion of the continental shelf. Three-dimensional baroclinic forecasts and hindcasts (right) conducted since fall 2000 often extend north to British Columbia and south to California to account for the effect of upwelling and downwelling regimes due to winds alongshore (Baptista et al. 2005).

comparison allows a continued understanding of the capabilities and limitations of the model, which has led to better predictions over a time period.

A complementary product, generated more sporadically, consists of monthlong hindcasts of depth-averaged circulation. We complete these simulations retrospectively using a larger computational grid, extending from the Bonneville Dam to the Pacific Ocean (Figure 35). Boundary conditions are imposed based on observations rather than predictions of the external forcings. Prior to the beginning of this review, monthlong hindcasts were available for 1997 and part of 1998.

The ability to represent water levels and velocities with good spatial resolution, for long periods of time and within reasonably controlled quality, allows us to explore patterns and trends of physical behavior and estuarine habitat opportunity for juvenile salmon in the modern Columbia River system. We can process the model-generated data to evaluate indices of physical performance of the estuary and apply these results to interpret fisheries data.

The computation of these indices is flexible in time and space, because model results are available at small intervals (15 minutes) and as a pseudocontinuum within the computational grid. Indices for spatial patterns and seasonal and interannual trends can be conveniently analyzed relative to external forcings such as river flow. We also can perform model simulations and calculate associated indices for predevelopment (historical) conditions and future management scenarios. Thus the model offers an analytical tool for evaluating past and future effects of various management actions on estuarine habitat.

One goal of this report was to explore the feasibility of using CORIE modeling products to characterize modern variability and historical trends in the physical habitat of the Columbia River. We focused on concepts and methods for utilizing simulation databases to analyze the influence of estuarine physical habitat on salmon life history and performance in the estuary. These preliminary outcomes will need to be revised and extended in the future. The robustness and extent of the circulation simulation database can and should be increased over a time period. The findings of this investigation, therefore, should be considered as guiding hypotheses rather than established protocols.

One of the challenges faced in this investigation was the definition of indices of physical habitat most relevant to salmon and to the member/vagrant hypothesis (see the "Conceptual Framework for Evaluating Estuarine Habitat Conditions," section, page 21). After several iterations, we selected indices of habitat opportunity, including:

- threshold depths and velocities for subyearling salmon,
- residual velocities, and
- hydrodynamic residence times.

The concept of modeling indices of physical habitat opportunity is novel, but it provides a natural link between estuarine physics and interpretation of ecological and fisheries data. The concept involves a simple binary decision about whether the physical habitat is favorable to juvenile salmon, as defined in this technical memorandum by water velocities, depths, or both. Specifying the criteria for favorable conditions is more challenging. The rationale for this specification is discussed in the "Establishing Criteria for Habitat Opportunity" subsection.

Residence times and residual velocities are conventional indices of physical estuarine behavior that reflect net transport. As defined in this investigation, they relate strictly to net hydrodynamic transport (i.e., they are not tied to any particular biological or ecological tracer, and thus do not reflect self-propelling motion or deposition/erosion processes). Each index integrated water motion over space or time. In the case of residence times, integration is over space and time, along the path of a parcel of water as it leaves the estuary. In the case of residual velocities, integration is over a multiple of a tidal period, at a fixed position in space.

Establishing Criteria for Habitat Opportunity

Juvenile salmon respond to a variety of habitat characteristics that collectively affect their migration behavior through estuaries, including abiotic (i.e., temperature, salinity, and turbidity) and biotic conditions (i.e., prey availability). The emphasis on species with subyearling life histories, particularly Chinook and chum salmon, defines specific limits for model simulations distinct from those that would apply to larger stream-type migrants.

Depth

Subyearling salmon, migrating through estuaries as fry or fingerlings, tend to restrict their movements to shallow water until they reach larger sizes required to exploit deeper channels, open-water habitats, and associated prey resources (Groot and Margolis 1991). Chum and Chinook fry prefer shallow-water areas; at sizes ranging from 30–60 mm FL (millimeters fork length), both species occupy tidal wetland sloughs and channels, mud and sand flats, or beaches (Healey 1982 and 1991, Simenstad et al. 1982, Salo 1991). At 55–60 mm FL, chum fry often move into deeper offshore waters (Bax et al. 1980, Simenstad and Salo 1982). Subyearling Chinook may occupy estuarine marsh and other shallow-water habitats until they exceed 100 mm FL (Healey 1982, Levy and Northcote 1982). Various investigations suggest that salmon fry and fingerlings often remain within water depths between approximately 10 cm and 2 m. While admittedly there is considerable variation in fish movements, and salmon can and do migrate outside this range, we chose this depth window as a reasonable criterion for simulating estuarine habitat opportunity for subyearling, ocean-type Chinook.

Velocity

The opportunity for salmon fry and fingerlings to access estuarine habitats also may be determined by their swimming performance and the energetic constraints of maintaining position against tidal or river currents. We defined velocity, therefore, as a second criterion for simulating habitat opportunity for salmon fry and subyearlings.

Juvenile salmonids swimming performance is a function of fish size (body length); duration of swimming activity, including sustained versus burst speeds; and various environmental variables, including temperature and dissolved oxygen (Hoar and Randall 1978). Beamish (1978) reviewed swimming performance of fish from various laboratory studies, including sustained swimming speeds, defined as speeds that fish could maintain for long periods (>200 minutes) without muscle fatigue. Davis et al. (1963) reported sustained swimming speeds of 23–67 centimeters per second (cm s^{-1}) for 81–126 mm Chinook salmon at an acclimation temperature of 11.5°C. For somewhat smaller subyearling Chinook (51–73 mm FL) acclimated at 15°C, maximum sustained swimming speeds ranged from 29 to 53 cm s^{-1}. Based on these results, 30 cm s^{-1} was chosen as a threshold velocity for modeling the availability of low velocity rearing habitat for subyearling Chinook within the Columbia River estuary. To assess model sensitivity to different assumptions of habitat suitability, we also evaluated habitat opportunity using a 50 cm s^{-1} threshold velocity.

Simulation Scenarios, Methods, and Uncertainty

The two-dimensional circulation database used in the present investigation is summarized in Table 9. The database includes simulations for modern and predevelopment bathymetry and for modern and predevelopment river flows. Simulations for the modern system cover 1997 and 1998, the first five months of 1999, and selected months in the spring of 1980. Simulations for the predevelopment system include selected months in 1880 typically associated with high (May, July) or low (December) river flows. The 1880 simulations were often conducted for two alternative bathymetries, as discussed in the "Creation of the Bathymetric Database" subsection. In some cases, 1880 bathymetry and 1997 river flows were combined in an attempt to separate the effects of change in river flow from effects of bathymetric change.

The 1997 and 1998 simulations already were available for our analysis, but other simulations were necessary. The process used in all simulations was similar, and involved the steps described in the following subsections.

Choice of the Computational Domain

The modern and predevelopment systems were represented from Bonneville Dam to the Pacific Ocean (Figure 35). Our incorporation of shallow peripheral areas in the computational domain for the modern and the predevelopment systems is not fully consistent.

Creation of the Bathymetric Database

Generating the bathymetric database for the computational domain is a resource- and time-consuming task. We realized early in the project that resources were insufficient to

Table 9. Summary of two-dimensional simulation database for bathymetric and velocity analyses. Simulation months are online at http://www.ccalmr.ogi.edu/bpa/simulations.html.

1880	1880*	1880**	1980	1997	1998	1999
				January	January	January
				February	February	February
				March	March	March
			April	April	April	April
May	May	May	May	May	May	May
				June	June	
July		July		July	July	
				August	August	
				September	September	
				October	October	
				November	November	
December	December			December	December	

* Simulations with predevelopment bathymetry (sensitivity to vertical datum interpretation, as described in the appendix of Sanders et al. 2000).

** Simulations with predevelopment bathymetry but with 1997 river flows.

generate two bathymetric databases. Therefore we used the existing CORIE representation of modern bathymetry and concentrated our efforts on a careful reconstruction of predevelopment bathymetry. While this decision was critically important to make this investigation feasible, comparisons between modern and predevelopment bathymetrics require several assumptions.

The modern CORIE bathymetry (Figure 36) was generated in 1996, when modeling emphasized the circulation dynamics of the deeper regions of the estuary (e.g., navigation and north channels). The bathymetric base for the entire estuary utilizes National Oceanic and Atmospheric Administration (NOAA) survey results from the period in 1958, but it is overridden in the channel and vicinity by the 1996 USACE surveys (Sanders et al. 2000). While shallow areas are represented in this base map, assumptions for regions without survey data (in particular, island formations, such as in Cathlamet Bay) tend to overestimate depth.

The Geographic Information System (GIS)-based process followed the generation of the predevelopment bathymetry (Figure 37). Careful analysis of historical bathymetry relied on informed assumptions when survey data were unavailable. Areas of uncertainty typically focused around island formations (Figure 38). To test the sensitivity of the characterization of physical estuarine habitat to our bathymetric assumptions, we created a second predevelopment bathymetric coverage (Figure 39) that probably overestimated water depth around island formations. This overestimation roughly approximates that of the modern CORIE

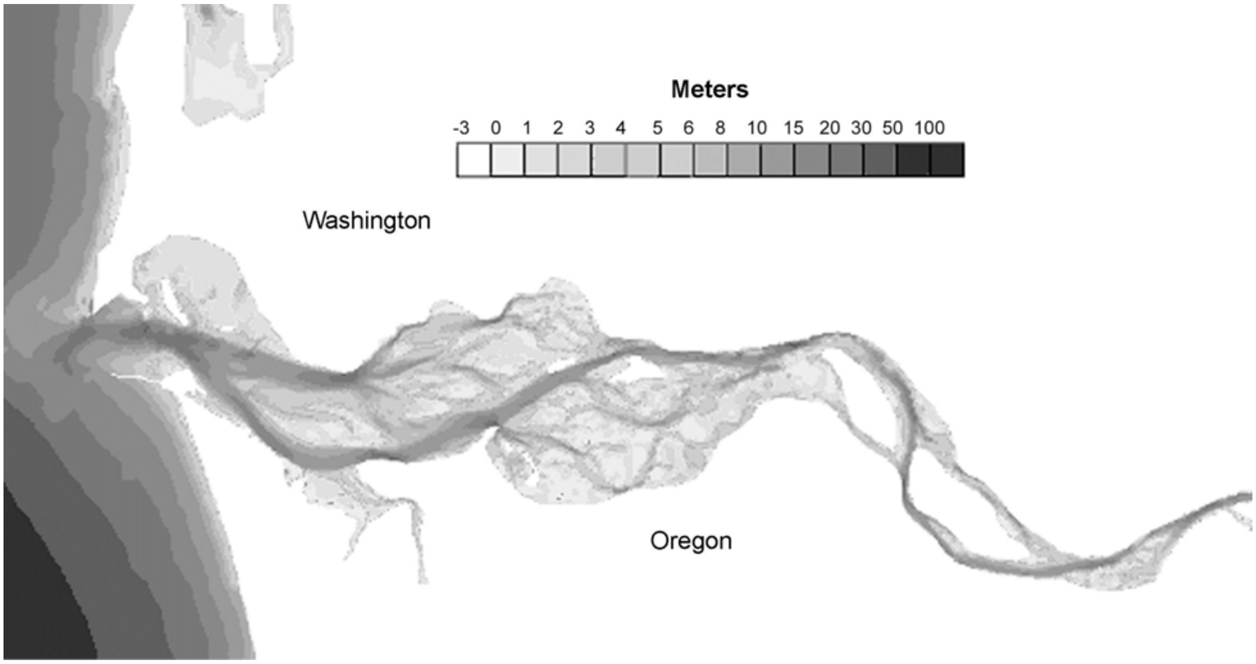


Figure 36. A model of bathymetry for the Columbia River estuary. Modern and predevelopment model bathymetry were derived at different times, with different modeling purposes and support technologies. The darker shades are areas with greater depths. Modern model bathymetry predates this study, without focus on detailed representation of very shallow areas (e.g., in Cathlamet Bay), which may be deeper than in reality. Outside the navigation channel area of influence (where there are modern USACE surveys), this bathymetry is based on surveys from the late 1950s.

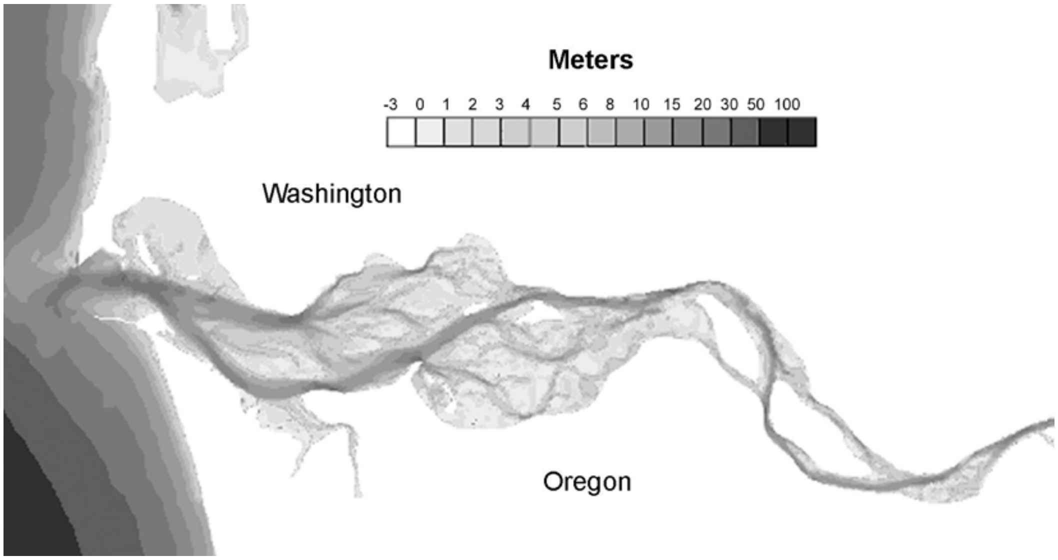


Figure 37. A model of predevelopment bathymetry of the Columbia River estuary. It is based on surveys from the 1870s and 1880s. The darker shades are areas with greater depths. While the density of the survey points is smaller than for the modern bathymetry, more sophisticated GIS techniques were used to render the bathymetry, and more care was used in representing shallow areas as accurately as allowed by survey data (Sanders et al. 2000).

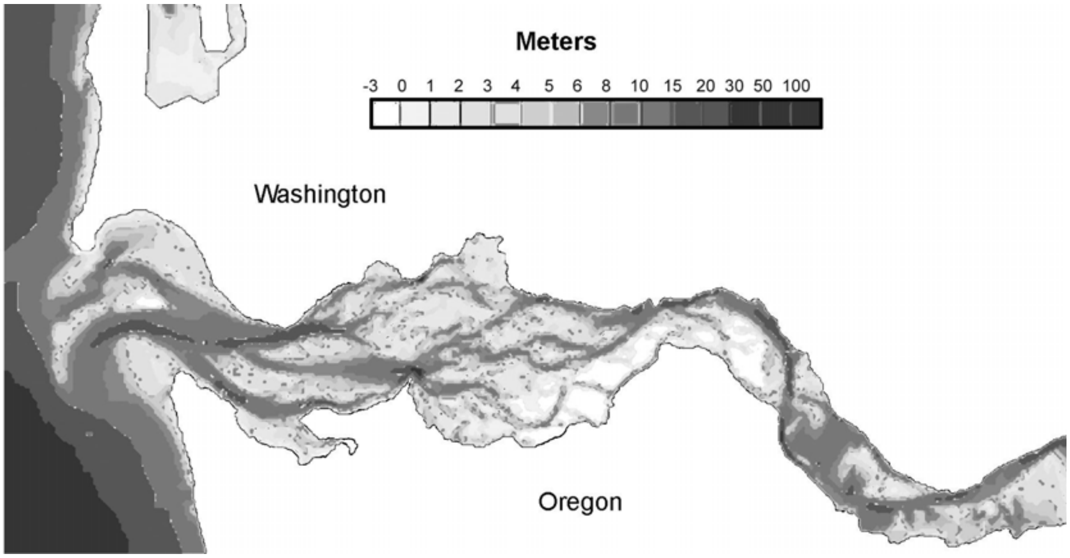


Figure 38. A model of corrected bathymetry for the Columbia River estuary predevelopment system. The darker shades are areas with greater depths. Corrected bathymetry involves introducing controlled changes to enable an analysis of the sensitivity of habitat opportunity to the uncertainties in bathymetry (Sanders et al. 2000).

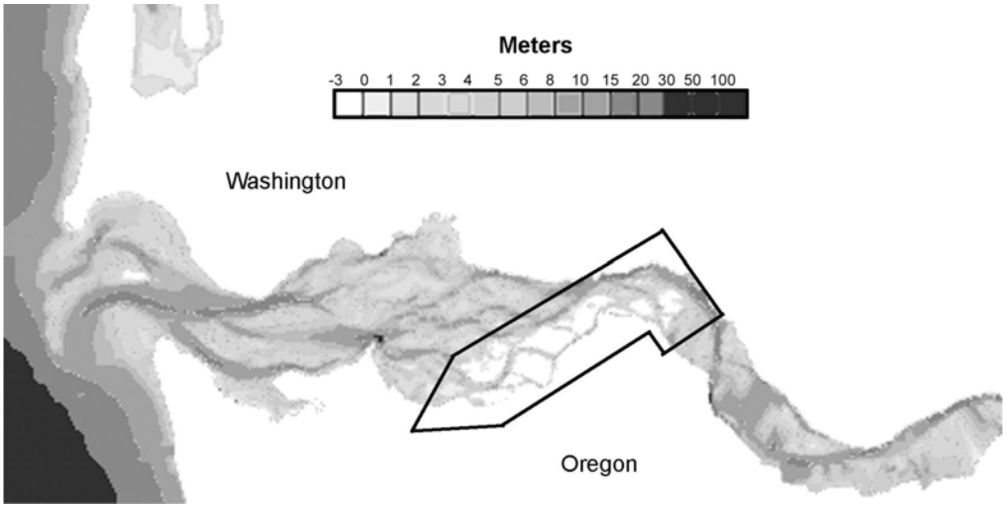


Figure 39. A model of Columbia River estuary predevelopment bathymetry. The polygon bounds the area affected by the changes introduced to create the corrected bathymetry. The changes tend to deepen the Cathlamet Bay area and are described in detail in Sanders et al. 2000.

bathymetry and allows us to test the sensitivity of the model to alternative assumptions about historical depths.

Creation of a Computational Grid

The hydrodynamic model used in this study (see the "Simulation Model" subsection, page 98) solves the conventional shallow-water equations (partial differential equations reflecting conservation of mass and momentum) in an unstructured computational grid formed by triangular elements (Figure 35). Generation of this grid requires positioning the computational nodes (the vertices of the triangles) over the domain in ways that reflect the desired level of resolution (which typically varies from region to region of the domain). Higher resolution is sought in areas representing high gradients in bathymetry or water circulation.

Specification of Boundary Conditions

Prior to any simulation, external forcings must be specified at the boundaries of the computational domain. The barotropic circulation in the Columbia River estuary is primarily controlled by two external forcings: ocean tides and river flows.

For the period of simulation, we specified tides by harmonic synthesis of tidal constituents derived from the eastern North Pacific Ocean tidal model of Myers and Baptista (2000). David Jay and co-workers provided representative flows at the Bonneville Dam, in the Willamette River, and in the Cowlitz River (see the "Changes in Hydrological Conditions" section, page 47).

Simulation Model

We conducted simulations with ADCIRC, an advanced circulation model developed at the U.S. Army Corps of Engineers Waterways Experimental Station in Vicksburg, Mississippi (Luettich et al. 1991, Luettich and Westerink 1995). The two-dimensional version of the model is used in this analysis with options enabled for treatment of wetting and drying. We calibrated and validated the model for the modern system (part of the CORIE modeling procedures). A verified model that properly reflects current conditions presumably will depict accurately the historical estuary within the limits of uncertainty for bathymetry and external forcing.

Analysis of the data was consistent across simulations, and typically involved:

- calculation of indices (residence times, residual velocities, and habitat opportunity) at the nodes or elements of the computational grid, and typically as a function of time,
- spatial mapping of indices, either for the entire domain or subregions,
- integration of indices, across time or space or both, in the latter case over the entire domain or subregions, and
- correlation of integrated indices with river flows at Bonneville Dam.

Modeling, whether for modern or predevelopment conditions, has inherent errors and uncertainties that are challenging to overcome, especially for a complex system such as the Columbia River. The CORIE infrastructure approaches this challenge with a long-term perspective. Each new application or research project contributes incrementally to extend modeling capabilities, database coverage, reliability, and awareness of modeling limitations.

This investigation focused on extending modeling capabilities (through the creation of a predevelopment bathymetry and through the systematic creation of indices of physical habitat opportunity and net hydrodynamic transport) and database coverage (through simulation of selected months in 1880, 1980, and 1999). Some modeling limitations also were identified, and will be discussed. It was beyond the scope of this investigation, however, to identify modeling uncertainty systematically or to improve the inherent quality of the hydrodynamic simulations. Important goals of the simulations reported in this section are:

1) to evaluate this new method for assessing estuarine habitat opportunity, and
2) to understand the relative sensitivities of the model to changes in physical variables, principally depth and river flow.

Results

Habitat Opportunity

For each of the three criteria identified, we computed hours of habitat opportunity (defined as hours within a month in which the criterion is met locally) for each node of the computational grid, for all available months in the simulation database, and we normalized the results to 720-hour months. Isolines of the resulting normalized habitat opportunity for the entire estuary were plotted for each (predevelopment and modern) month of the simulation database. Isolines for May 1997 are shown in Figure 40.

To facilitate the analysis, we divided the estuary into six regions of distinct characteristics relative to topology, bathymetry, and distance to the ocean (Figure 41):

- Region 1, Baker Bay
- Region 2, the lower estuary
- Region 3, Youngs Bay
- Region 4, Cathlamet Bay
- Region 5, Grays Bay
- Region 6, the upper main stem of the estuary

Within each region we computed integral indicators of habitat opportunity as weighted averages over the appropriate portion of the computational domain. Habitat-opportunity isolines were drawn for each region and month (e.g., Figure 42 shows Cathlamet Bay in May 1997). We also computed differences of habitat opportunity relative to selected reference months (May 1997, July 1880, May 1880, and May 1880* with adjusted predevelopment bathymetry, [Table 9]) and drew the resulting isolines (e.g., Figure 43). We plotted the seasonal variation of integral indicators of habitat opportunity (Figures 44, 45, 46, and 47), as well as the relationship of these indicators to river flow (Figures 48, 49, 50, and 51) to compare the responses of different regions and of modern and predevelopment systems.

The results constitute a massive amount of information from simulations of habitat opportunity (for depth and velocity criteria), retention times, and residual velocities for various combinations of historical and modern bathymetry and river flow. In the following subsections we synthesize the results for each criterion and discuss the implications.

Velocity criterion

Several distinct patterns and trends emerge in the characterization of habitat opportunity based on the velocity criterion. Habitat opportunity correlates strongly with river flow, but the results are distinct for the various regions under consideration (Figure 41) and for the modern and predevelopment systems (Figure 48). Habitat opportunity is highest in Region 3 (Youngs Bay) and Region 1 (Baker Bay), the two lateral bays closest to the ocean, and tends to decrease in an upstream direction. Habitat opportunity is high to moderate, clearly decreasing with increasing river flow, in Region 4 (Cathlamet Bay) and Region 5 (Grays Bay), two lateral bays located upstream in the estuary. Habitat opportunity is moderate to essentially nil in Region 6 (the upper estuary) and decreases sharply with river flow. Habitat opportunity is low in Region 2 (the main stem of the lower estuary) and insensitive to river flow.

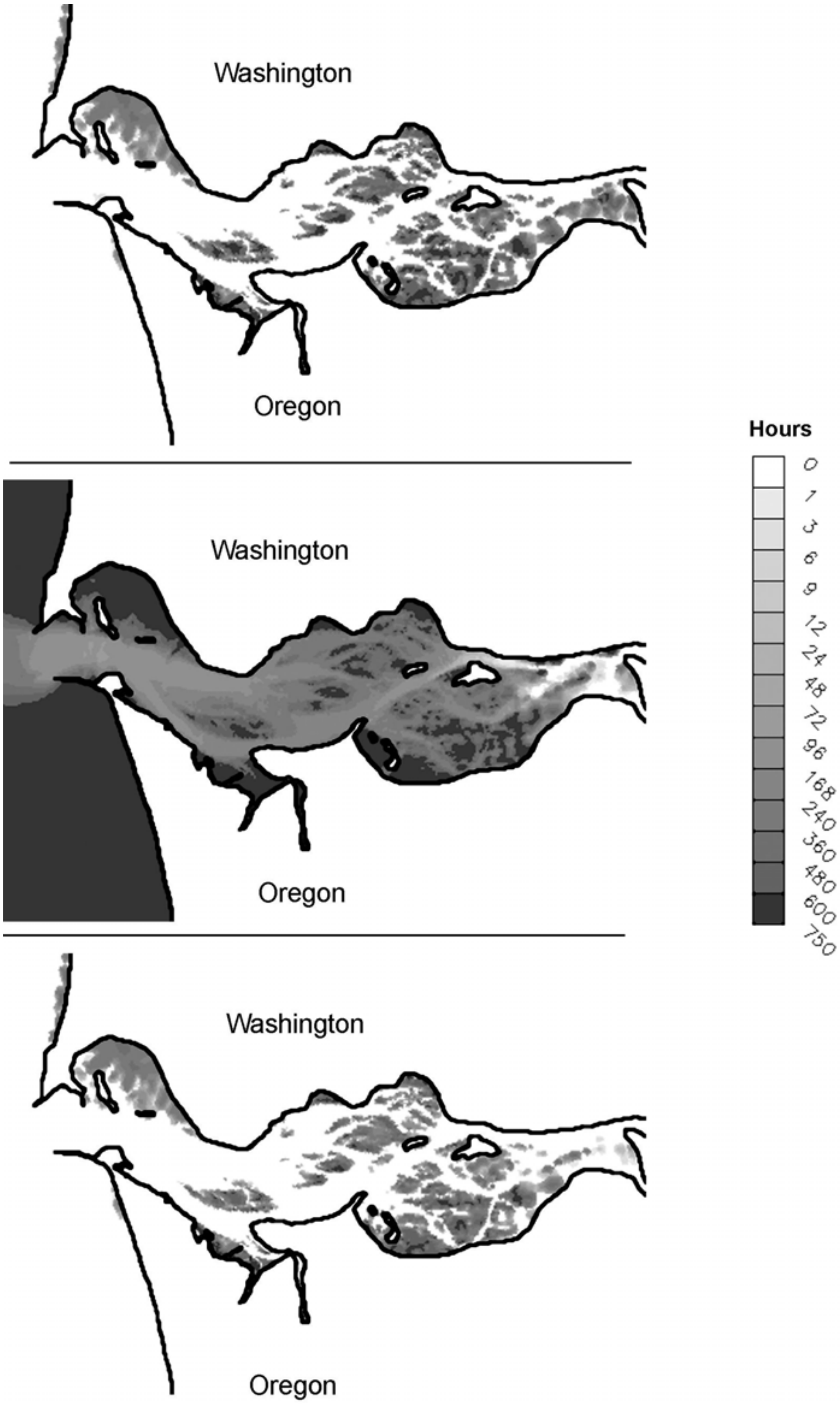


Figure 40. Isolines of Columbia River estuarine habitat opportunity for May 1997, in hours normalized to a 30-day month, using depth (top), velocity (middle), and combined criteria (bottom). When combined, depth criterion is a stronger factor than velocity criterion, which leads to similarities in the patterns of the darker gray areas between depth and combined criteria in the bottom panel. May 1997 is online at http://www.ccalmr.ogi.edu/~ppearson/BPA5/1997-May.html. Other months are online at http://www.ccalmr.ogi.edu/~ppearson/BPA5/habitat.html.

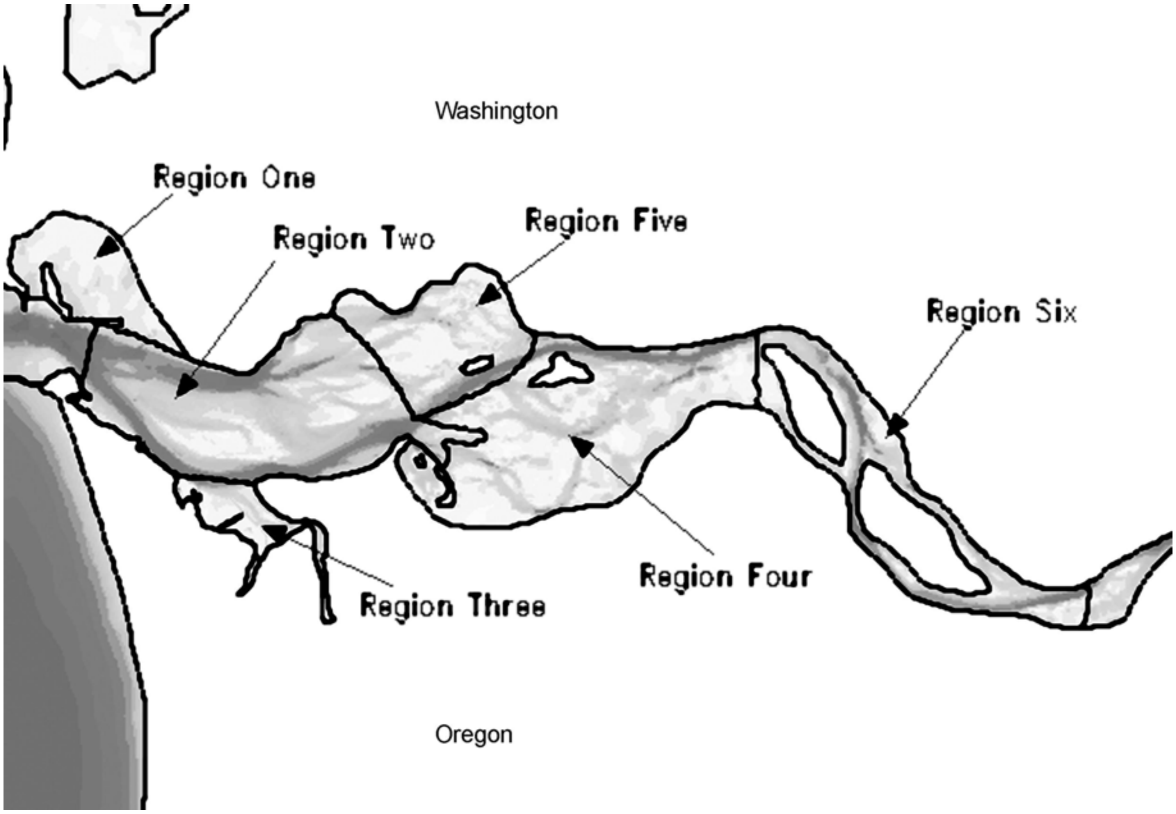


Figure 41. Different environments in the Columbia River estuary offer distinct habitat opportunity. In an attempt to capture differences in trends and patterns, the estuary was divided into the subregions shown for rough consistency with a prior CREDDP study. Online at http://www.ccalmr.ogi.edu/bpa/habopp_synthesis.html.

Habitat opportunity in the modern and predevelopment estuaries is not fundamentally different in Regions 1, 2, and 3 (Figure 49). However, in Regions 4 and 6 the predevelopment opportunity is significantly higher and much more resilient to increases in river flow. The change in Region 4 is noteworthy, given the amount of potential wetland rearing habitat available in that region for subyearling Chinook salmon. Changes between predevelopment and modern habitat opportunity with river flow were less apparent in Region 5. This difference is worth further investigation and may be related to a disproportionate effect of the channel contained within Region 5.

Seasonal variability of habitat opportunity also is distinct from region to region. In Regions 4, 5, and 6, where opportunity decreases with river flow in the predevelopment and modern systems, freshet periods consistently provide the lowest habitat opportunity (Figure 44). In Regions 1, 2, and 3, freshets also offer minimum opportunity in the predevelopment system, but this is not the case for the modern system, where seasonal patterns are ambiguous.

Interannual variability appears largely associated with river flow, with one notable exception: in Regions 1 and 3, habitat opportunity in 1997 is largely uncorrelated with that for 1998 and 1999. For this reason modern habitat opportunity in Regions 1 and 3 shows anomalous scatter (Figure 49 and Figure 50). We find no explanation for this behavior, and we recommend

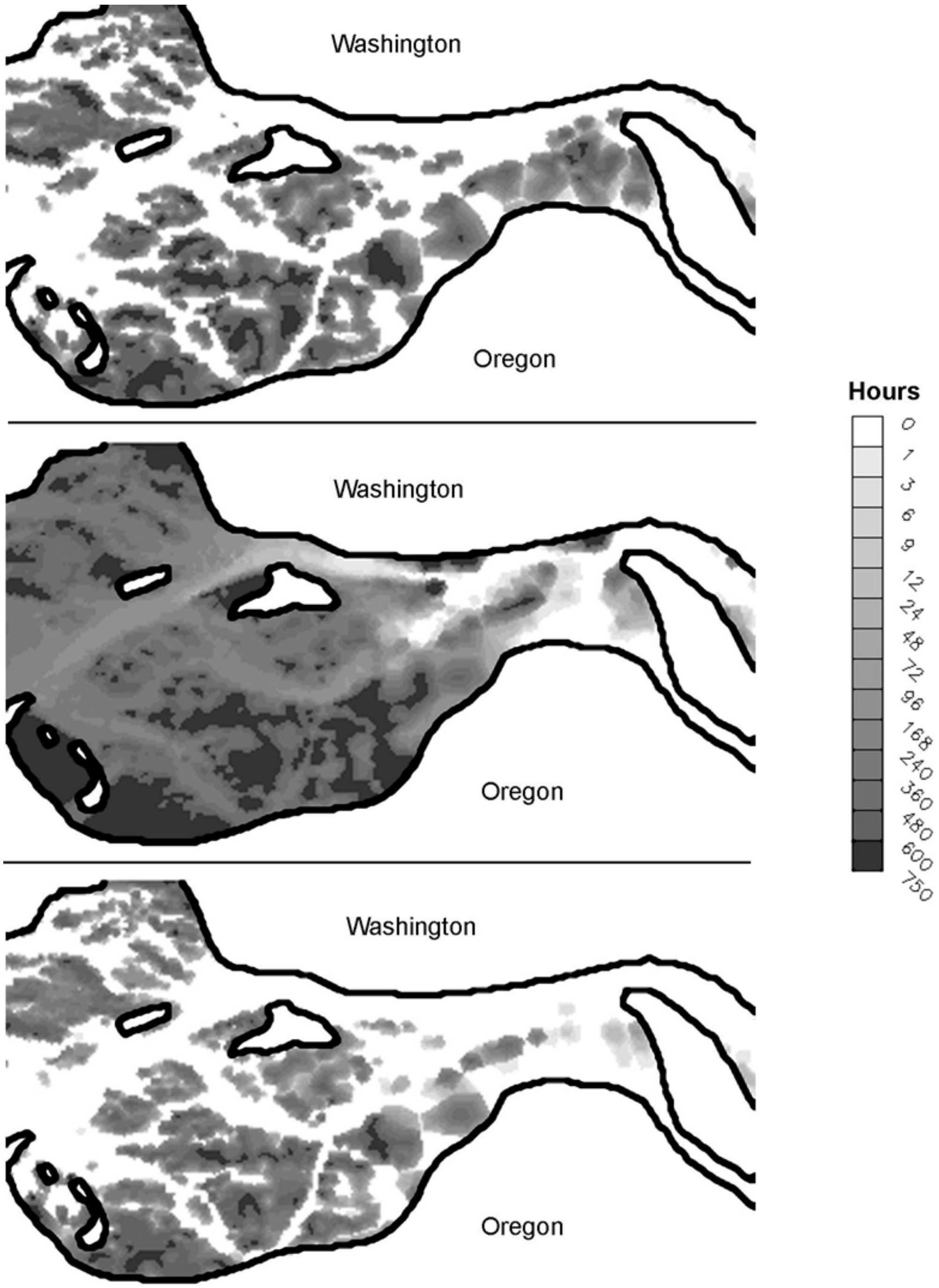


Figure 42. Isolines of habitat opportunity in Region 4 for May 1997, in hours normalized to a 30-day month, using depth (top), velocity (middle), and combined criteria (bottom). The lighter shades in the combined criteria constitute optimum habitat relative to primary and secondary channels. May 1997 is online at http://www.ccalmr.ogi.edu/~ppearson/BPA5/REG4-HST1997-May.html. Other months are online at http://www.ccalmr.ogi.edu/~ppearson/BPA5/habitathist.html.

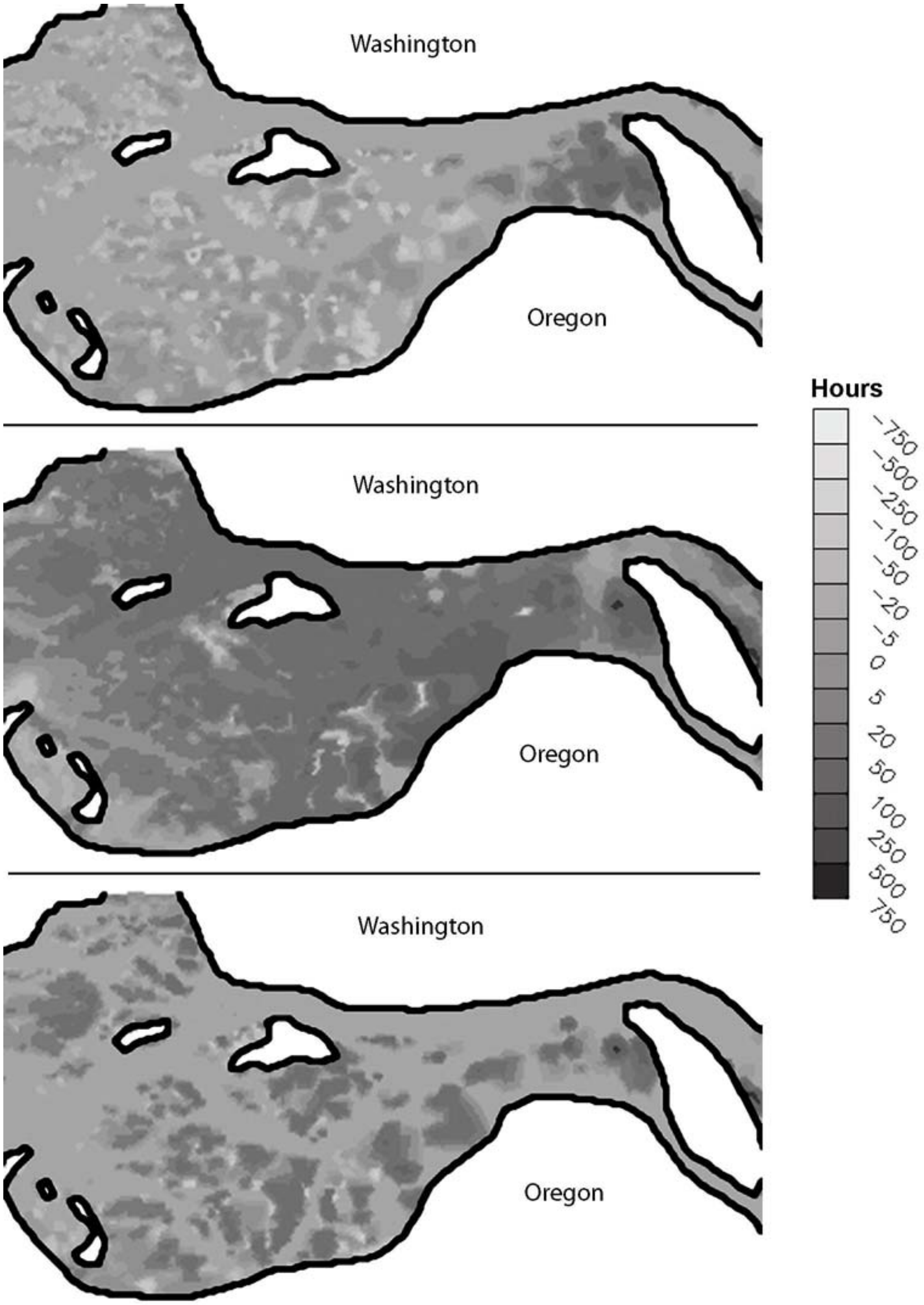
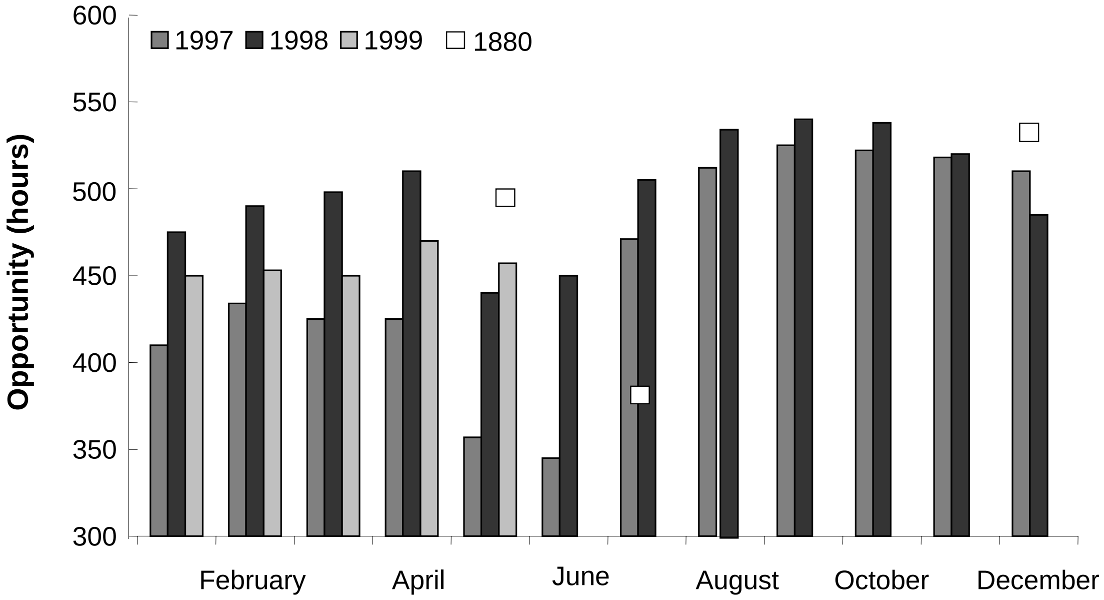


Figure 43. Isolines made by comparing the differences in Columbia River habitat opportunity available in Region 4 (July minus May 1997), in hours normalized to a 30-day month, using depth (top), velocity (middle), and combined criteria (bottom). Darker areas are positive values (clearly dominant under any criteria) and represent higher opportunity in July, which has lower river flows. This month is online at http://www.ccalmr.ogi.edu/~ppearson/BPA5/REG4-HST 1997-July.html. Simulations for all months listed in Table 9 and for all subregions are online at http://www.ccalmr.ogi.edu/~ppearson/BPA5/habitathist.html.



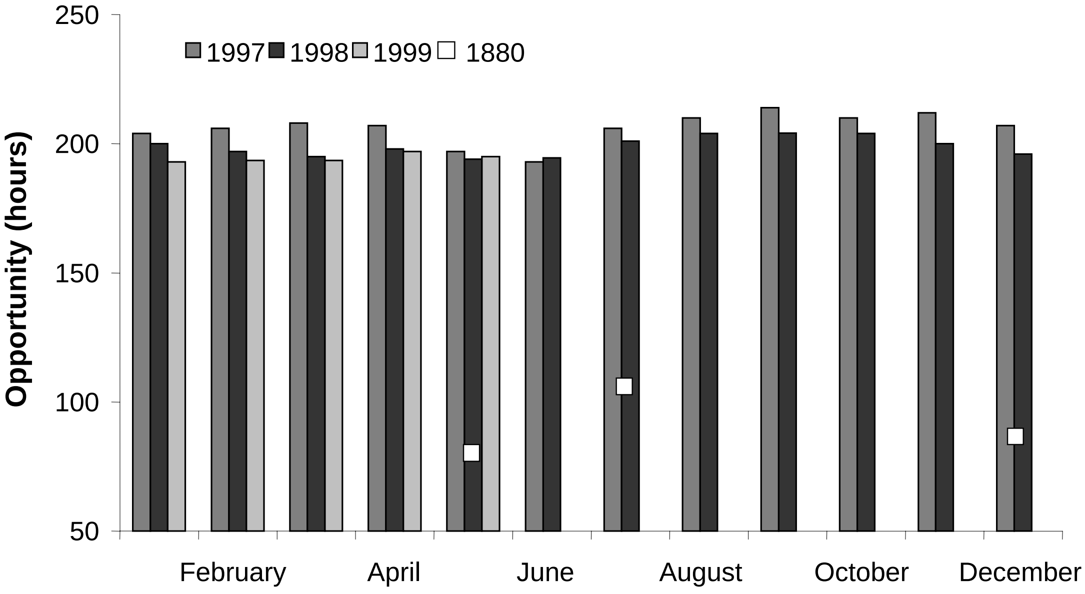


Figure 44. Seasonal variation of Columbia River estuarine habitat opportunity in Region 4 for velocity (top) and depth (bottom) criterion. Habitat opportunity is shown in hours normalized to a 30-day month. Habitat opportunity based on the velocity criterion shows marked minima during freshet season. Velocity criterion is online at http://www.ccalmr.ogi.edu/bpa/newfigures/R4velsea.gif. Depth criterion is online at: http://www.ccalmr.ogi.edu/bpa/newfigures/R4velsea.gif. Simulations for all subregions and criteria are available at http://www.ccalmr.ogi.edu/bpa/habopp_synthesis .html.

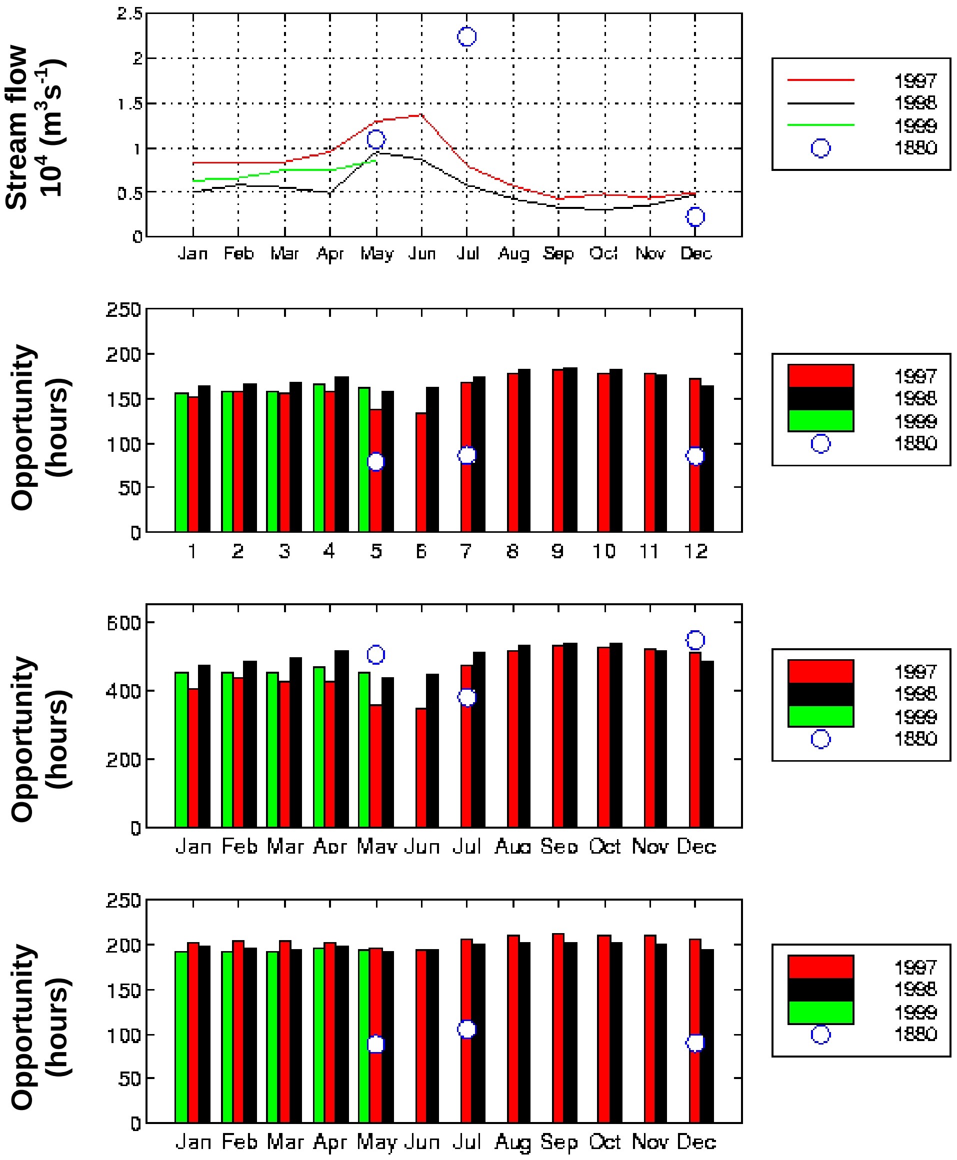


Figure 45. River flow and seasonal variation of Columbia estuarine habitat opportunity in Region 4 for modern versus predevelopment systems (criterion from top to bottom: river flow, combined, velocity, and depth). Habitat opportunity is shown in hours normalized to a 30-day month. Habitat opportunity based on the velocity criterion but not on the depth criterion shows marked minima during freshet season.

that this aspect be further investigated, because it might help explain the contrast between El Niño (as in 1997) and non-El Niño years. While the possibility that a numerical or processing artifact is biasing the results cannot be excluded, there was no evidence of such.

Temporal shifts in freshets from June to July in the predevelopment system to May/June in the modern system (see the "Changes in Hydrological Conditions" section, page 47) correlate with shifts in the periods of minimal habitat opportunity in the middle and upper estuary, that is, in the subregions where the correlation of opportunity with river flow is strongest (Figure 44).

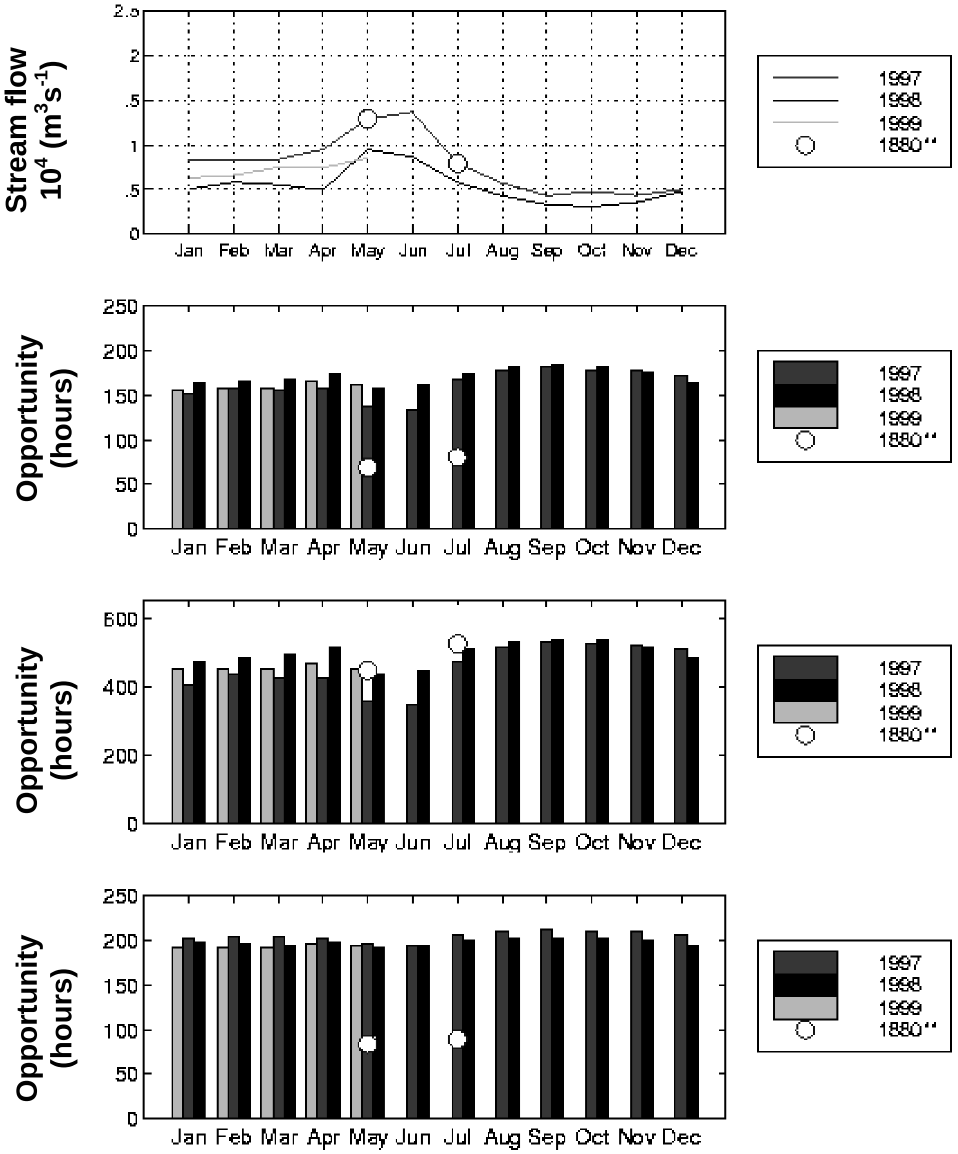


Figure 46. River flow and seasonal variation of Columbia River estuarine habitat opportunity in Region 4 (criterion from top to bottom: river flow, combined, depth, and velocity) for modern bathymetry and flows (1997–1999) and predevelopment bathymetry with 1997 flows (1880** refers to simulations listed in Table 9).

Excluding local detail, habitat opportunity based on the velocity criterion appears only modestly sensitive to the controlled bathymetric modification introduced in Region 4 (Figure 51). Although only indirectly, this suggests that the criterion is robust regarding one of the known weaknesses of the circulation model: representation of modern bathymetry in very shallow areas.

Habitat opportunity is sensitive to the value chosen for the velocity criterion (Figure 52). The 30 and 50 cm s^{-1} criteria applied were within the range of literature values that Beamish

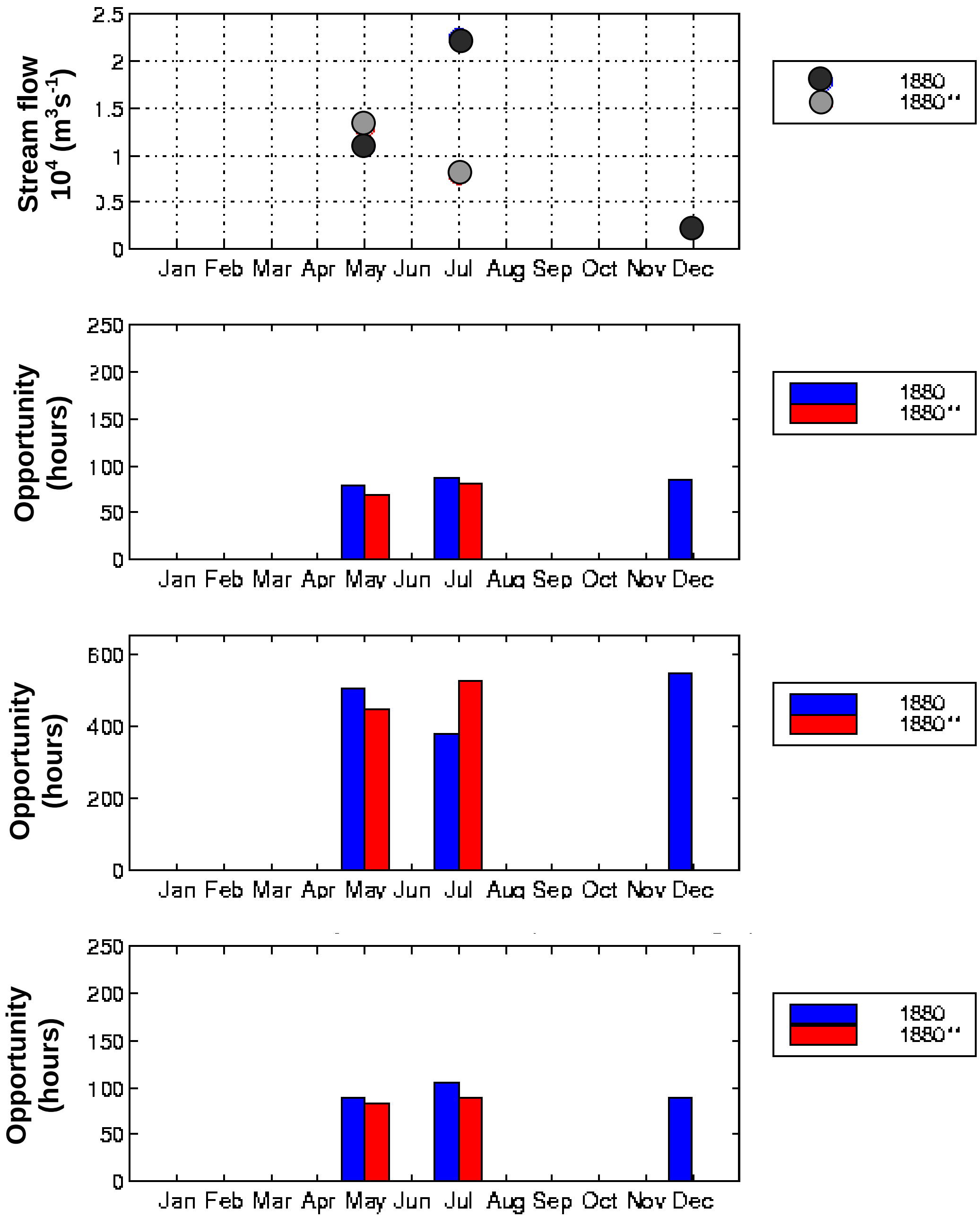


Figure 47. River flow and seasonal variation of Columbia River estuarine habitat opportunity in Region 4 (criterion from top to bottom: river flow, combined, depth, and velocity) for predevelopment bathymetry and flows (1997–1999) and predevelopment bathymetry with 1997 flows (1880** refers to simulations listed in Table 9).

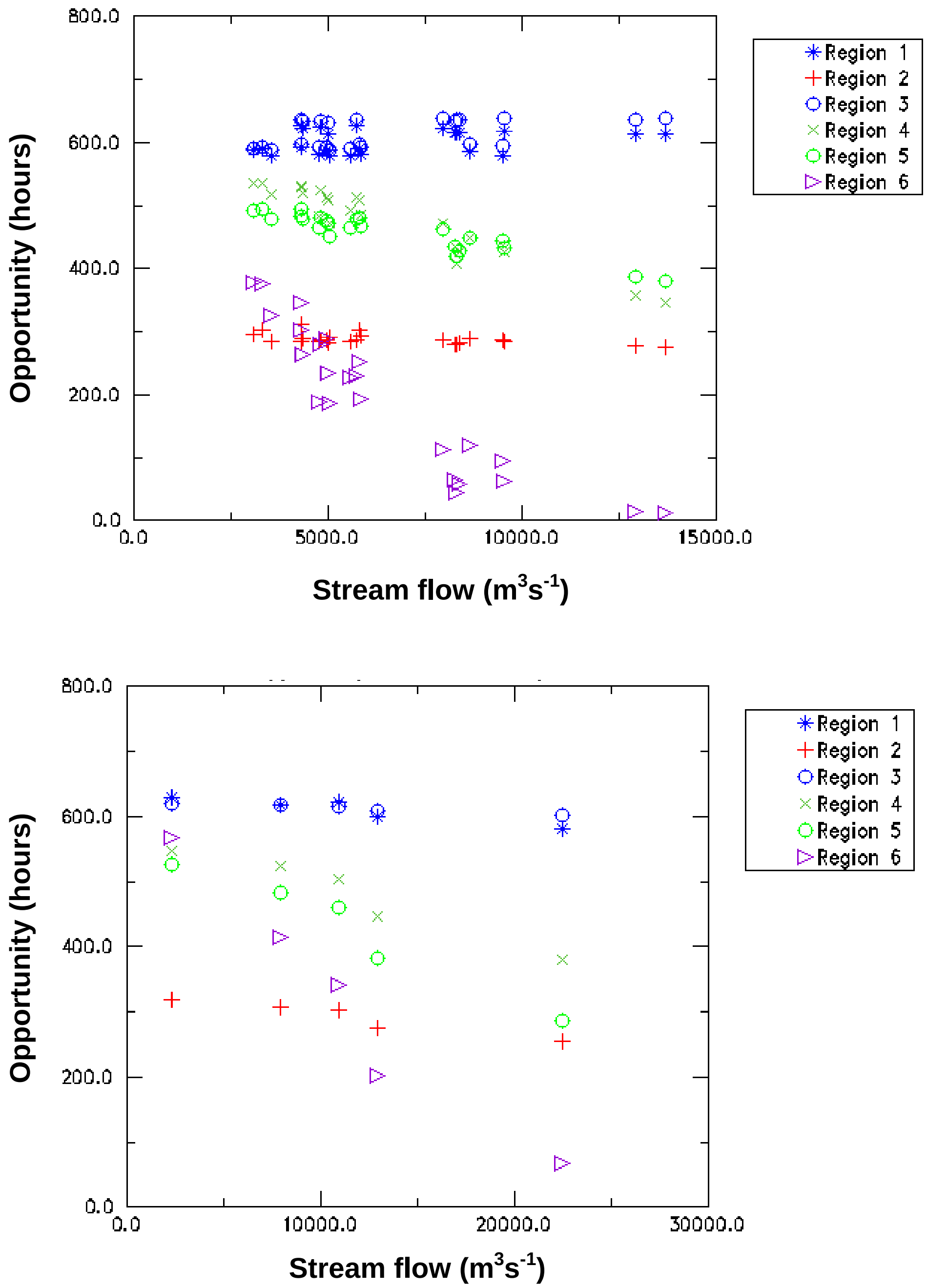


Figure 48. Columbia River estuarine habitat opportunity as a function of river flow, for the modern (top) and predevelopment (bottom) systems. Habitat opportunity shown in hours normalized to a 30-day month is based on the velocity criterion. Different subregions provide distinct habitat opportunity and have distinctive correlations with river flow. The modern system is online at http://www.ccalmr.ogi.edu/bpa/newfigures/velsynthesis.gif and the predevelopment system is at http://www.ccalmr.ogi.edu/bpa/newfigures/velsynthold.gif. The online database contains plots for the depth and combined criteria at http://www.ccalmr.ogi.edu/bpa/habopp_synthesis.html.

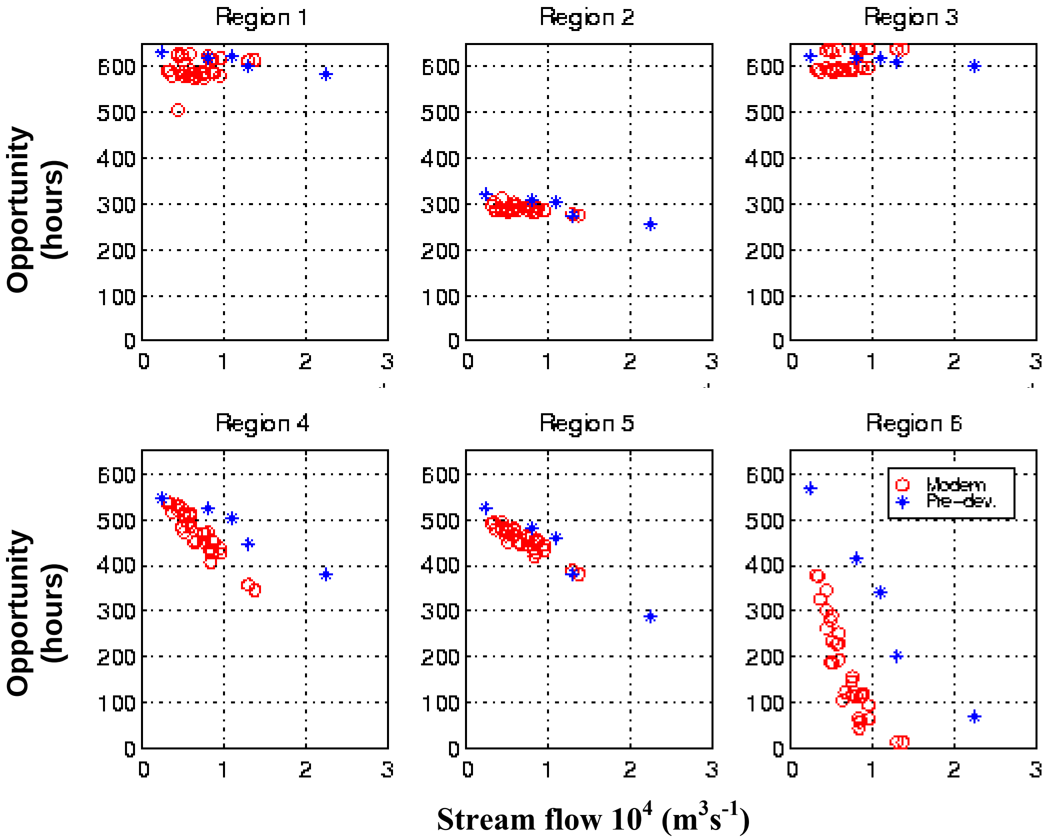


Figure 49. Region-by-region comparison of predevelopment and modern estuarine habitat opportunity as a function of river flow, for the velocity criterion. In Regions 1, 2, 3, and 5, the habitat opportunity is similar. In Regions 4 and 6, the differences are recognizable. The x-axis in all regions represents stream flow 10^4(m^3s^{-1}).

(1978) reported for sustained swimming speeds of subyearling Chinook salmon. A limited analysis suggests that the alternative threshold velocities yield different absolute estimates of habitat opportunity under varying flow conditions. Yet the general decreasing trend in habitat opportunity with increasing river flows did not change with threshold velocity (Figure 52).

Depth criterion

Distinct patterns and trends also emerge in the characterization of habitat opportunity based on the depth criterion. We explored these patterns and trends in less detail than was shown for the velocity criterion, because the weak representation of shallow-water bathymetry in the modern estuary may have limited the robustness of this criterion.

Results indicate a high degree of sensitivity of habitat opportunity to the controlled modification of predevelopment bathymetry in the shallowest Region 4 areas. Artificially deepening that bathymetry greatly increases habitat opportunity (Figure 51). The important, albeit indirect, implication is that modern habitat opportunity based on the depth criterion is substantially overestimated by our results: the model's modern bathymetry is least accurate (and

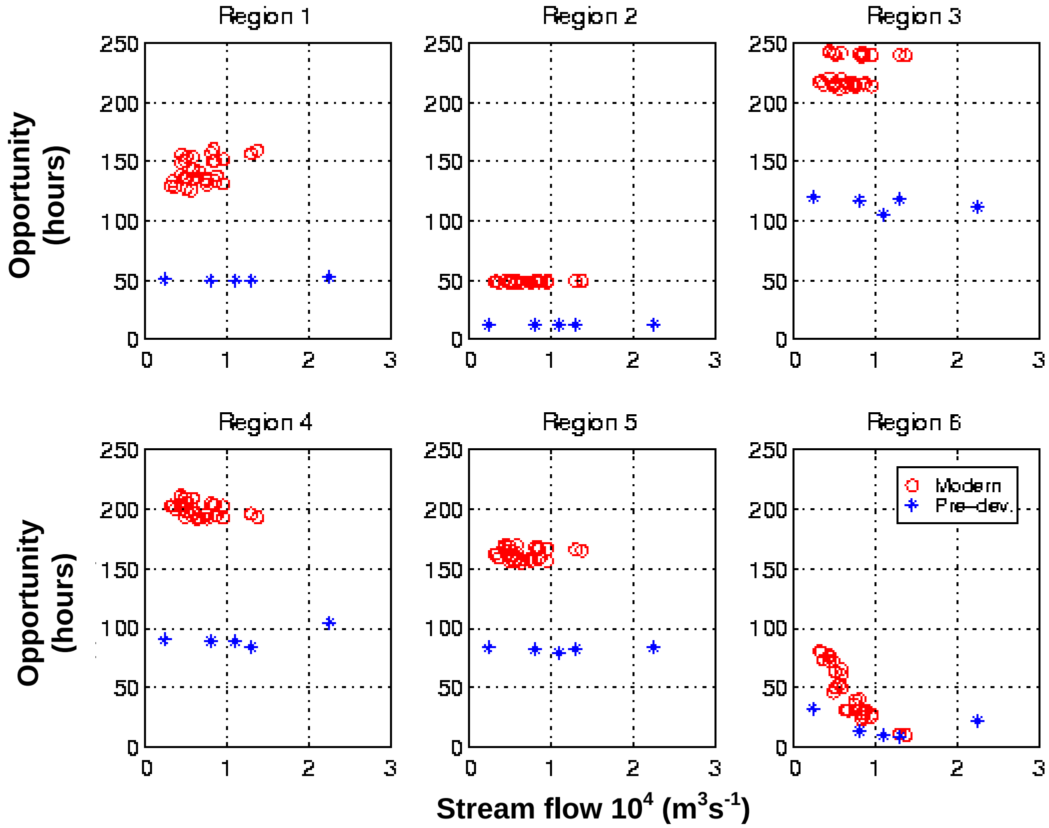


Figure 50. Region-by-region comparison of predevelopment and modern estuarine habitat opportunity as a function of river flow, for the depth criterion. Limitations in the representation of modern bathymetry may artificially limit opportunity in the modern system. The x axis in all regions represents stream flow 10^4(m^3s^{-1}).

artificially too deep) in the shallowest areas of the estuary. While Figure 50 shows the comparison between habitat opportunity in the modern and predevelopment systems based on this criterion, overestimation of modern opportunity strongly reduces the meaning of this comparison. The problem is solvable by correcting the modern bathymetry and redeveloping the simulation database, but that is not within the scope of this study.

Habitat opportunity in general is smaller when based on the depth criterion than on the velocity criterion. While the magnitude will vary, the sign of this difference appears unlikely to change when the modern bathymetry is corrected.

Plots of habitat opportunity versus river flow still enable separation of the different regions in which the estuary was divided in clusters of similar behavior. The composition and behavior of each cluster, however, differ from those of the velocity criterion. In particular, all lateral bays show modest sensitivity to river flow when habitat opportunity is defined by the depth criterion. Within the lateral bays cluster, habitat opportunity decreases progressively from Region 3 to Region 4/Region5 and Region 1. Thus proximity to the ocean is not driving the differences in regional habitat opportunity based on the depth criterion.

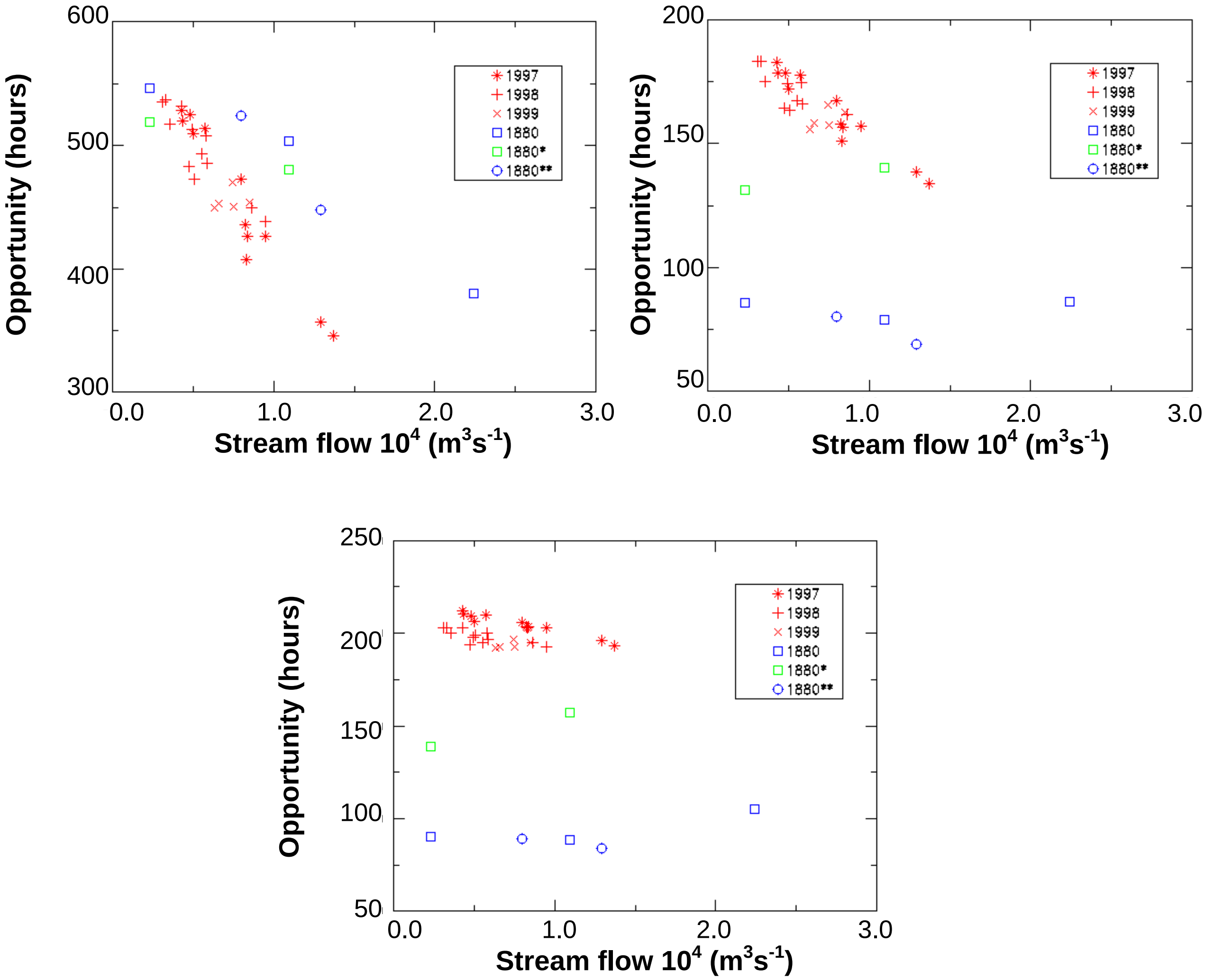


Figure 51. Columbia River estuary habitat opportunity in Region 4 as a function of river flow for velocity (top left), depth (bottom), and combined criteria (top right). Habitat opportunity shown in hours normalized to a 30-day month is based on the velocity criterion. There are marked differences between habitat opportunity in the modern and predevelopment systems. Sensitivity to controlled changes in bathymetry is much larger for the depth criterion than for the velocity criterion. Habitat opportunity for the depth criterion in the modern system is overestimated by weaknesses in the model bathymetry. For 1880* and 1880** see simulations listed in Table 9. The plot for velocity is online at http://www.ccalmr.ogi.edu/bpa/newfigures/R4vel.gif; depth is at http://www.ccalmr.ogi.edu/bpa/newfigures/R4elv.gif; and plot for combined criteria is at http://www.ccalmr.ogi.edu/bpa/newfigures/R4com.gif. Similar plots for other subregions are at http://www.ccalmr.ogi.edu/bpa/habopp_synthesis.html.

Combined Criteria

As illustrated for Region 4 (Figure 51), habitat opportunity defined by conditions when the velocity and depth criteria are met, is more restrictive relative to estimates for each individual criterion. Adding more criteria would probably increase this effect.

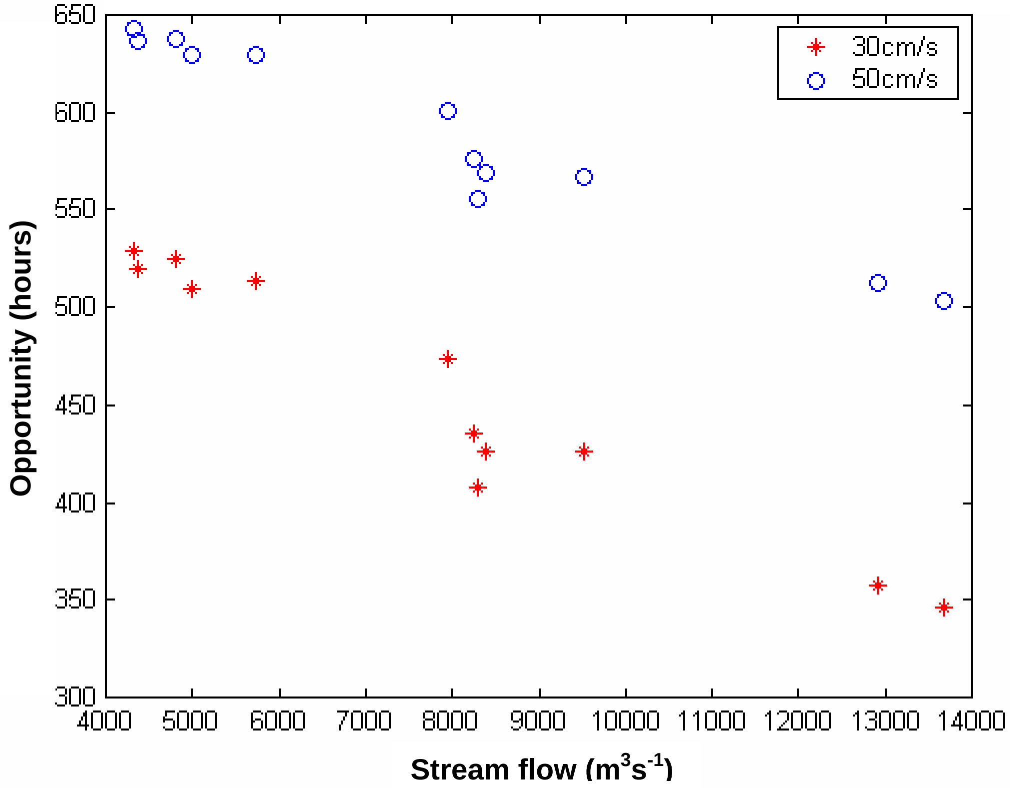


Figure 52. Sensitivity of habitat opportunity in modern Region 4 to the cut-off value of the velocity criterion (50 cm s^{-1} vs. the 30 cm s^{-1} used elsewhere in this work). Differences are significant, illustrating the need for integration of physically based criteria with biological data.

Meaningful combination of criteria requires that individual error/uncertainty is comparable for all individual criteria. This is not the case in this investigation, where bathymetric error/uncertainty affects the robustness of the depth criterion results much more than the velocity criterion results. Thus, while Figure 51 illustrates a potential approach for synthesizing information by applying multiple habitat criteria, the results may not provide an appropriate contrast between modern and predevelopment opportunity.

Figure 51 suggests the interesting hypothesis that the modern system may offer better habitat opportunity up to some critical flow range, beyond which the predevelopment system is superior. Before this hypothesis can be evaluated, however, a critical understanding of the true bathymetry in the shallow regions around the estuary's islands must be undertaken. This is not within the scope of the present exercise, but it represents a future analytical need.

Residence Times

Residence times are important descriptors of estuarine behavior (Pilson 1985, Zimmerman 1988). No real consensus, however, exists on the definition of residence time, mostly because the definitions are operational. The operational definition of residence times for this study is purely hydraulic, excluding consideration of settling/erosion or self-motion of the particles.

Sommerfield (1999) used the method proposed by Oliveira and Baptista (1997) to investigate residence times in the Columbia River. This method is based on time-consuming numerical simulations. Using preexisting numerical simulations of circulation, a large number of virtual particles are released inside the estuary and followed to determine the time that they take to leave the estuary. Information from individual particles, mapped at their starting locations, is then aggregated into estuary-wide isolines of residence times. Because of the previous work of Sommerfield (1999), and of the computation expense involved in the method, limited simulations of residence times were conducted (OGI 1999) for the modern estuarine bathymetry only.

The results supported Sommerfield's (1999) analysis and findings. Residence times in the estuary typically were short, often in the range of one to a few tidal cycles (Figures 53, 54, and 55). Even short residence times varied significantly in space, with the longest retention times for particles in shallow, constrained environments. Lateral bays are a prime example of a constrained environment in an estuary (Figure 53). Local freshwater inputs, which can significantly affect residence times in such constrained environments, are difficult to quantify and were not included in the simulations.

Residence times decreased with increasing river flow, but time of release and tidal coefficients introduced significant variation around this trend (Figure 54). Residence times were dependent on the time of release of the particles within a tidal cycle. This dependency is complex, and the notion that residence times are smallest for particle releases during ebb can be misleading depending on the location in the estuary (Figure 55). Aside from lateral bays, residence times tended to increase with distance from the mouth of the estuary (Figure 53 and Figure 56). Also, a time series of residence times in the upper estuary, particularly upstream from Tongue Point, exhibits much stronger evidence of tidal stirring and less organized flushing patterns (Figure 56).

The results just presented and in Sommerfield (1999) provide insights into patterns of variability of residence times in space and time that are important complements to our understanding of the net hydraulic transport in the Columbia River estuary. An indicator that is easier to calculate, however, was chosen to investigate net hydraulic transport (see the "Residual Velocities" subsection below), because it facilitated portrayal of the dependencies of natural system variability on postdevelopment changes.

Residual Velocities

Residual velocities are defined as the net velocity at a fixed point over a predefined time period that is typically a multiple of the tidal cycle. This Eulerian measurement is a complement and counterpart to residence times, which are inherently Lagrangian. Residual velocities characterize net hydraulic transport from the perspective of an observer fixed at a specific location, whereas residence times provide the perspective of an observer being passively transported by the water. Residual velocities are much faster to compute than residence times, given a preexisting simulation of the flow field, and results are easier to synthesize and interpret.

We computed residual velocities as month average for modern and predevelopment conditions across the entire simulation database (Figure 57). Within each month, we also

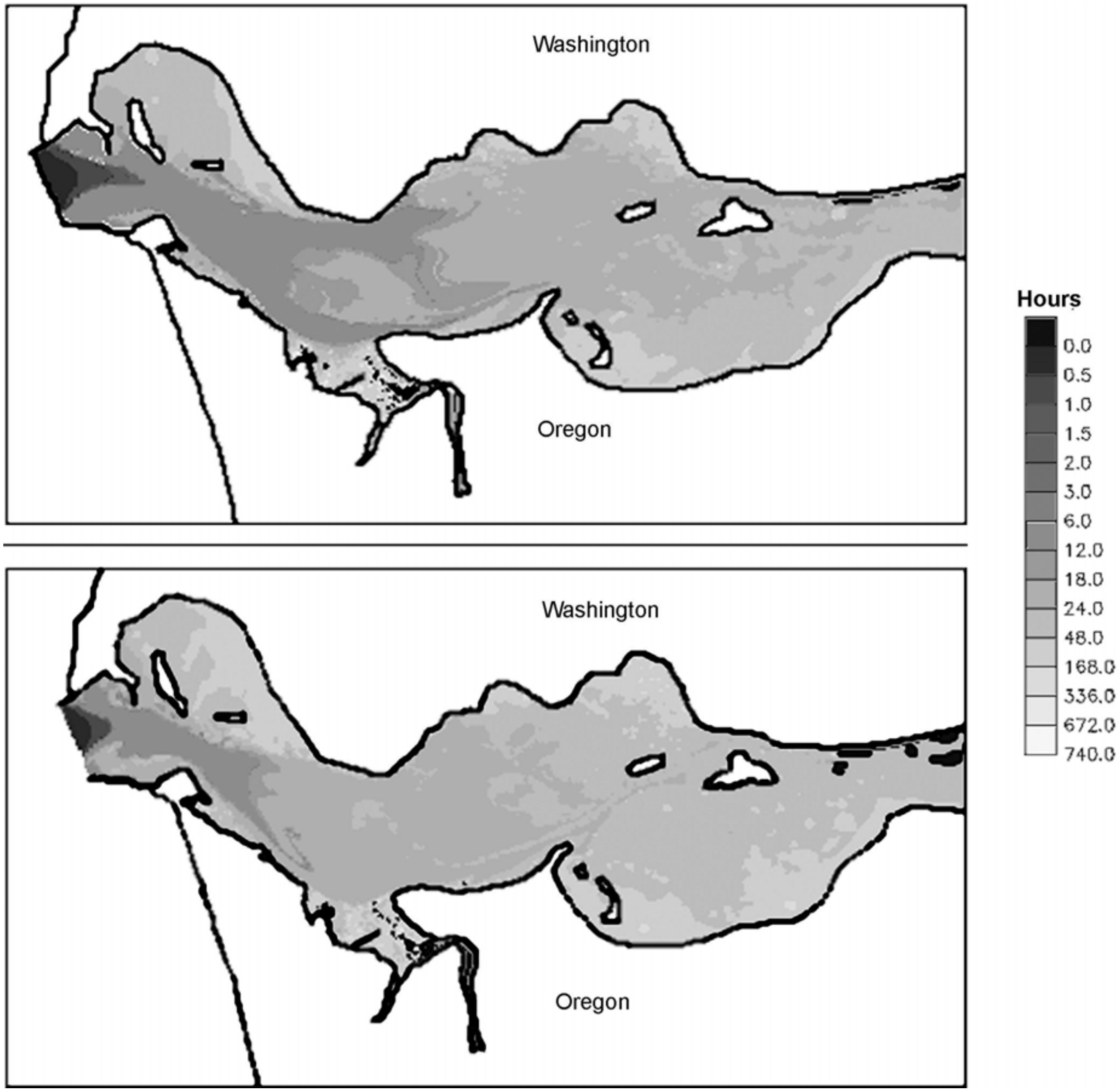


Figure 53. Residence times for high flow conditions (top) in June 1997 and for low flow conditions (bottom) in July 1997 in hours normalized to a 30-day month. Large percentages of the estuary have residence times of the order of one or a few tidal cycles. Lateral bays have substantially higher residence times than the main stem. The darker gray areas are noticeably bigger in the top panel, indicating residence times were lower in June 1997 than in July 1997. (Adapted from Sommerfield 1999.)

computed daily averages and estimated standard deviations. Isolines of monthly residual velocities and standard deviations are available as are plots that depict variations in residence times (integrated over the entire estuary) with season and river discharge (OGI 1999).

From estuary-wide integrated values, it becomes clear that residual velocities have significant seasonality, reflecting the seasonality of river flow (Figure 58). The residual velocities confirm analyses presented in the “Changes in Hydrological Conditions” section

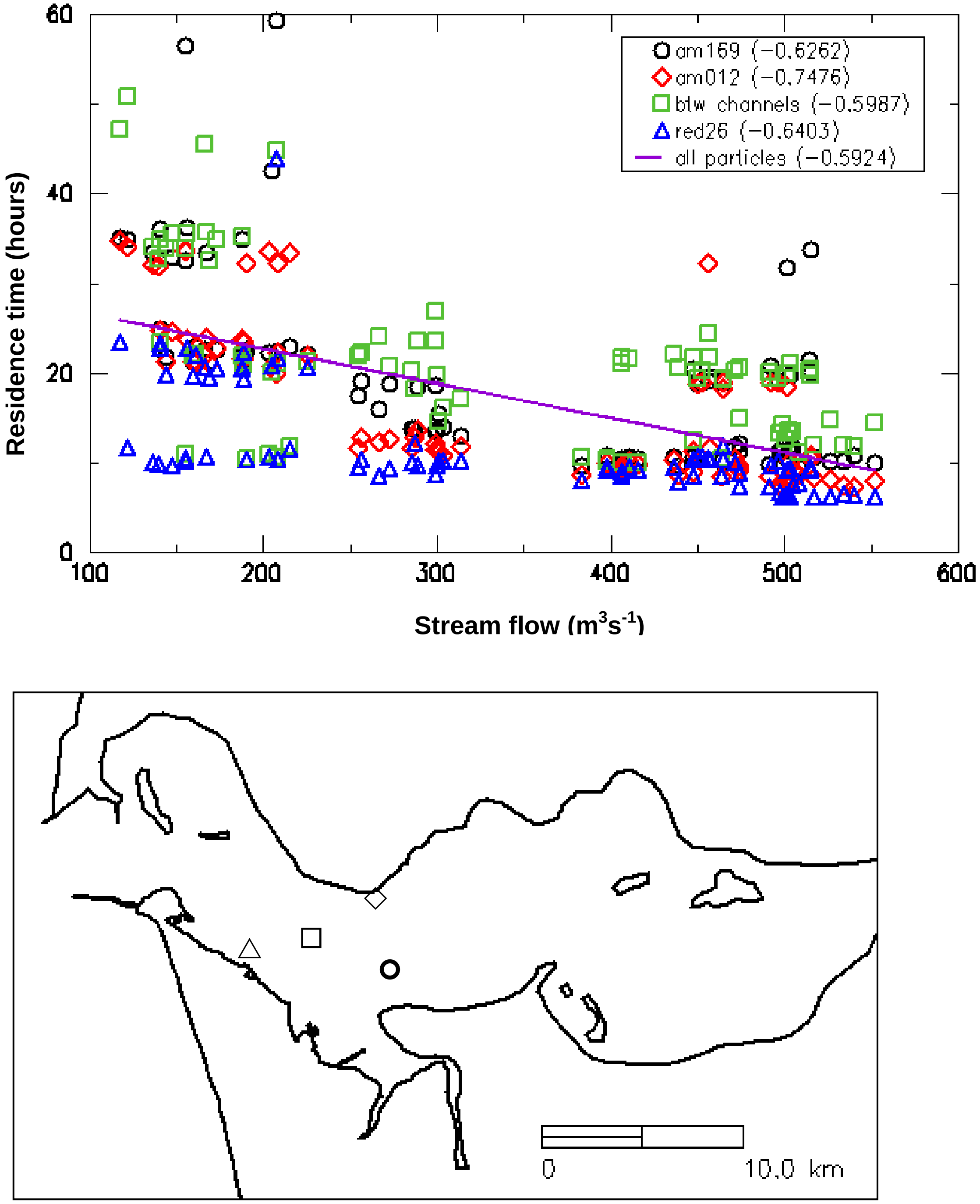


Figure 54. Influence of river flow on residence times, at four fixed locations in the estuary. The stations marked with a triangle and circle are in the navigation channel (near CORIE stations red26 and am169, respectively), the station marked with a diamond is in the north channel (near CORIE station am012), and the station marked by a square is in the shallow divide between channels. Results show that although residence times tend to decrease with increasing river flow, the correlation is complex, possibly because of tides and their nonlinear interactions with local topography and river flow. (Adapted from Sommerfield 1999.)

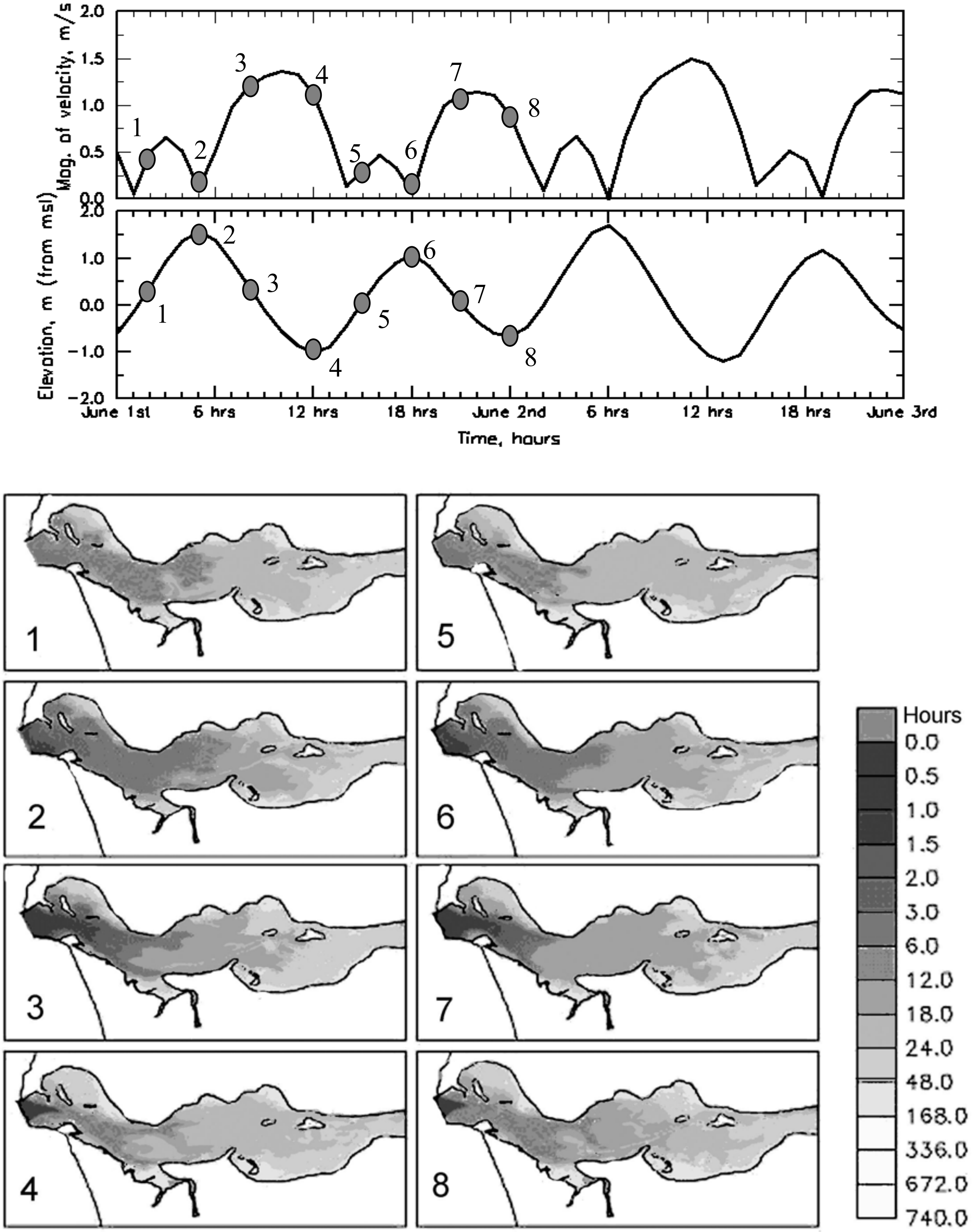


Figure 55. Residence times for June 1997 at eight release times over the tidal cycle. The lighter shades of gray represent areas with longer residence times. (Adapted from Sommerfield 1999.)

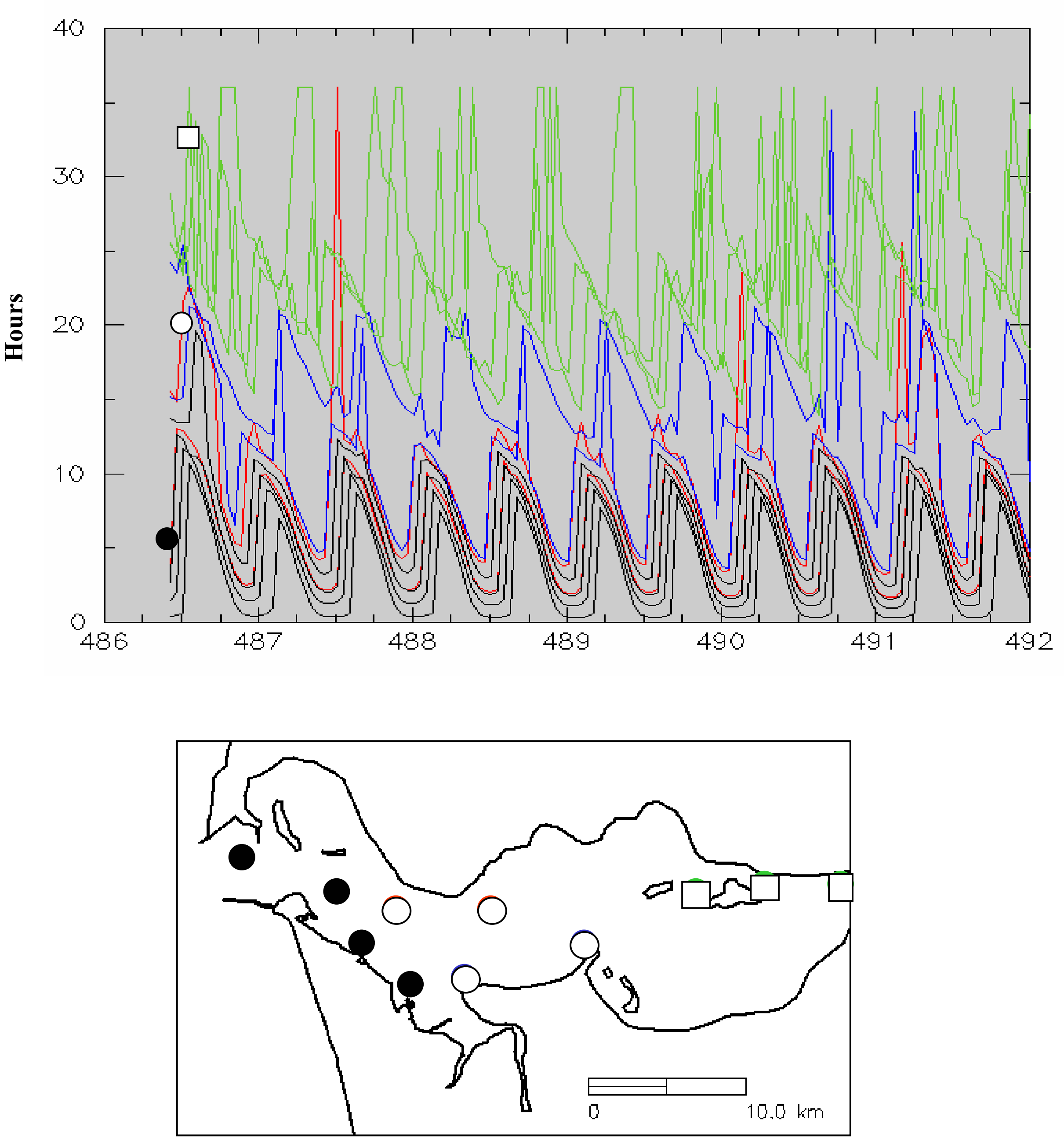


Figure 56. Time-series of residence times (in hours) for a 5-plus-day period in June 1997 at selected locations in the estuary. All locations (black dot, white circle, and square) are either in the navigation or the north channel (bottom). With increasing distance from the mouth, there is a progressive evolution from a tidal-controlled, quasiperiodic pattern of short (<12.4 hour) residence times to a more irregular pattern of residence times of the order of multiple tidal cycles (top, graph is cropped at 37.2 hours). This pattern of increasing disorganization toward the upper estuary reflects a higher opportunity of upper estuary, longer-residence-time particles to steer away from the main channels, in particular during tidal reversals. Black dot, white circle, and square (top) correlate to the nearby lines.

(page 47) that showed freshets occurred later in the predevelopment Columbia River estuary than in the modern system.

Seasonal trends indicate that residual velocities tend to increase with increasing river flow in an approximately linear manner (Figure 59). For the same river flow, the modern system exhibits higher residual velocities than the predevelopment system, likely reflecting a higher degree of canalization (i.e., fewer buffer regions) in the modern system. This suggests that net hydraulic transport is less sensitive to flow changes in the predevelopment estuary than it is in the modern estuary. The highest residual velocities, however, corresponded to July 1880, the highest flow month on the simulation database. Predevelopment freshets were more effective flushing events than modern freshets, even if the modern system is more canalized and more responsive to increases in river flow.

Estuary-wide residual velocities show little sensitivity to the controlled bathymetric changes introduced in the model for Region 4 (Figure 60). Local effects in the areas of bathymetric change are more significant, but uncertainties derived from not knowing the exact bathymetric configuration of the estuary in the predevelopment period appear to be a relatively minor concern. This finding is consistent with simulations of habitat opportunity based on the velocity criterion, which were similarly insensitive to bathymetric uncertainty.

Daily variations of residual velocities (as measured by standard deviations) are significant: for instance, local maxima in the standard deviation of the daily residual velocities exceed 15 cm s^{-1} in May 1880 (Figure 61). These daily variations follow correlations with river flow (Figure 61) that are similar to the pattern described for the monthly averages: trends in the variability of residual velocities increase linearly with river flow, and variations tend to be greater in the modern than the predevelopment estuary for a particular flow condition.

Implications for the Member/Vagrant Hypothesis

Our results illustrate that simulation modeling can be a useful tool to evaluate effects of spatial processes on salmon populations that are a central tenet of the member/vagrant hypothesis described in the “Conceptual Framework for Evaluating Estuarine Habitat Conditions” section, page 21. This tool is particularly suited to the Columbia River estuary, because the established CORIE observation network provides a means to refine and validate the hydrodynamic model continually.

Responses of the model to changing tides, river flows, and bathymetric conditions can be used to depict the range of alternative rearing and migration possibilities for salmon during their estuarine residency. Interactions among physical processes, including the basin-wide processes described in the “Changes in Hydrological Conditions” section, page 47, regulate estuarine circulation and, therefore, the distribution of physical conditions such as velocity, depth, temperature, etc. (Figure 62). The dynamics of these conditions, in turn, define the temporal and spatial sequence of habitat potentially available for salmon to express alternative rearing and migration behaviors.

The simple velocity and depth criteria we used to characterize habitat opportunities for salmon are limited by a lack of empirical data for salmon-habitat associations within the

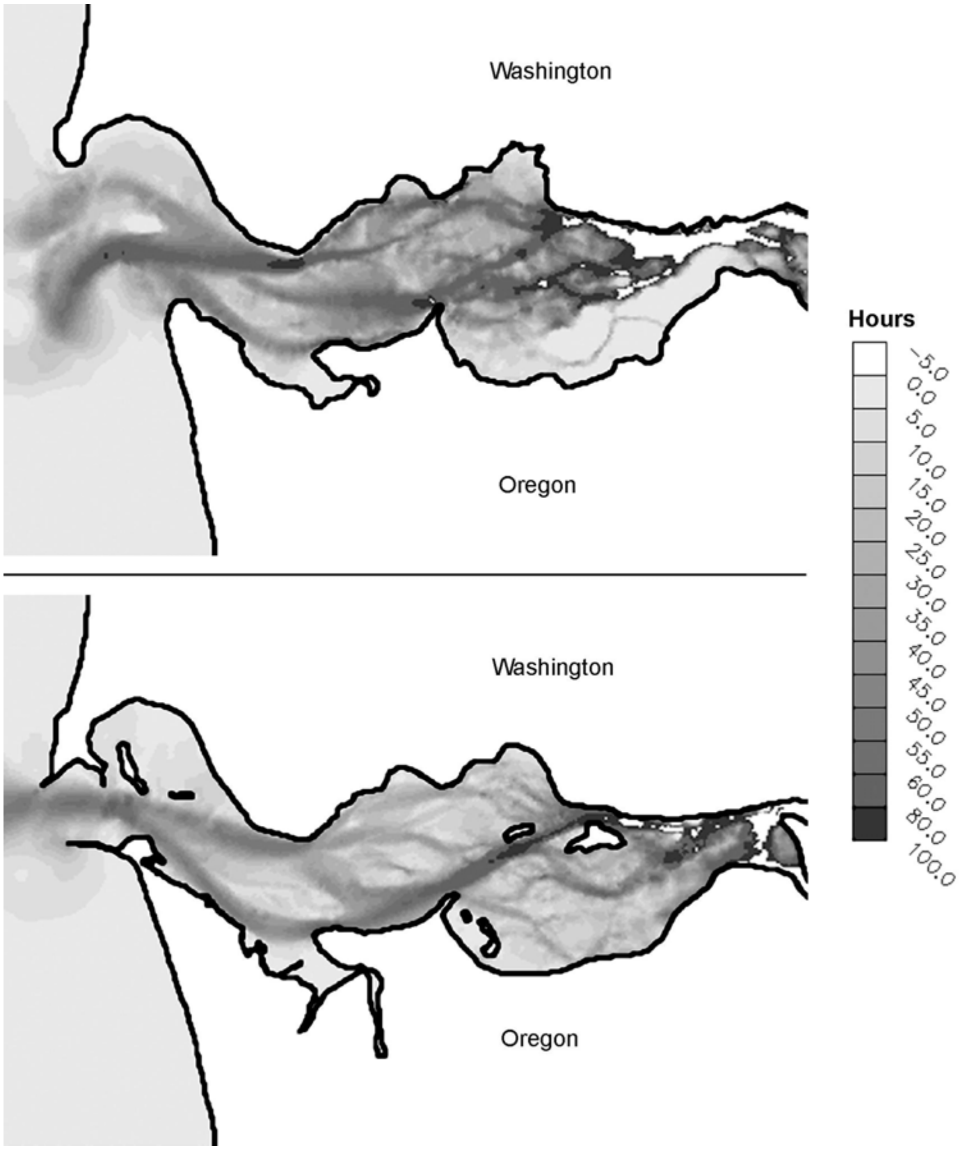


Figure 57. Residual velocities for high flow months in the predevelopment (top) and modern (bottom) systems. Differences follow closely the modifications in topology of the two systems, and in particular in the channel layout. Predevelopment is for July 1880 and modern is for May 1997.

Columbia River estuary. Nonetheless the model provides some useful insights into the physical dynamics of the estuary that may improve our ability to define the relevant constituents of salmon habitat.

Our results, for example, show that the velocity response to river flow varies among estuarine subregions. The suitability of particular geographic features (intertidal flats, marshes, and shore lands, etc.) for young salmon may depend on the hydrodynamics of the larger subregions within which each type of habitat is embedded. Subregional characteristics thus define distinct changes in the habitat-opportunity landscape as salmon pass from the narrowly constrained tidal river through the expansive intertidal wetlands of Region 4 and into the more

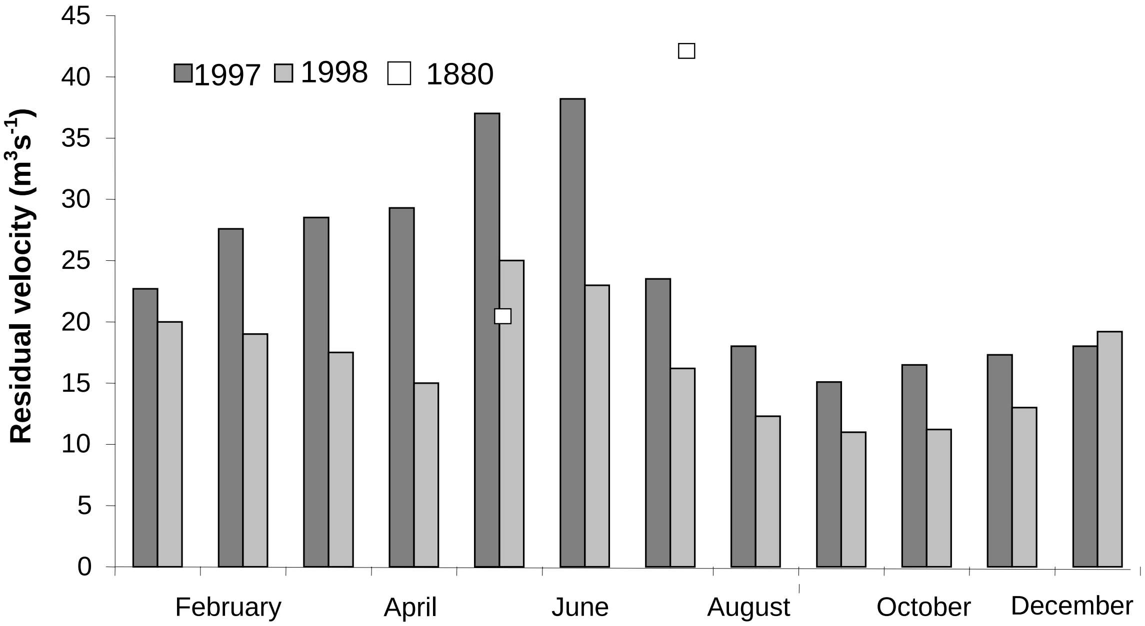


Figure 58. Residual velocities show marked seasonality, with highest values corresponding to freshet months. Freshets occurred later in the predevelopment system, a shift that is reflected in the residual velocities. There is a significant interannual variability (e.g., 1997 vs. 1998), with high flow years having larger residual velocities. All values of residual velocity shown in this figure are estuary wide, having been obtained by spatial integration of local values.

saline and highly energetic estuary mouth. Other physical parameters affected by estuarine circulation (e.g., salinity and temperature) could be evaluated similarly through model simulations if appropriate habitat-opportunity criteria for subyearling salmon can be defined.

Substantial changes in habitat dynamics could affect the expression of certain salmon rearing or migration behaviors associated with historic estuarine conditions. For example, significant changes in the timing of the spring freshet—a period of maximum velocities and minimum habitat opportunity—(see the “Changes in Hydrological Conditions” section, page 47) were reinforced by model predictions, particularly among upriver subregions that are most sensitive to flow variations. Thus in Region 4, minimum estuarine habitat opportunity based on our velocity threshold now occurs approximately one month later than during the predevelopment period (Figure 44). The effects of such change on salmonid life histories, including time and size at ocean entry, are uncertain.

A decrease in the resilience of upper-estuarine subregions to peak flows since the predevelopment period (Figure 51) is consistent with the apparent canalization of the estuary, including loss of peripheral wetland and floodplain habitats that may have afforded important off-channel refugia for salmon. While flood control from mainstem dams now minimizes spring peak flows, increased flow sensitivity as predicted by the model could limit rearing opportunities for small subyearling salmon in the upper estuary. Because historic floodplain and riparian habitats in these regions are poorly represented in the bathymetric data available for our simulations, the predicted decrease in habitat opportunity may be underestimated by our model results. In the “Change in Juvenile Salmon Life History, Growth and Estuarine Residence”

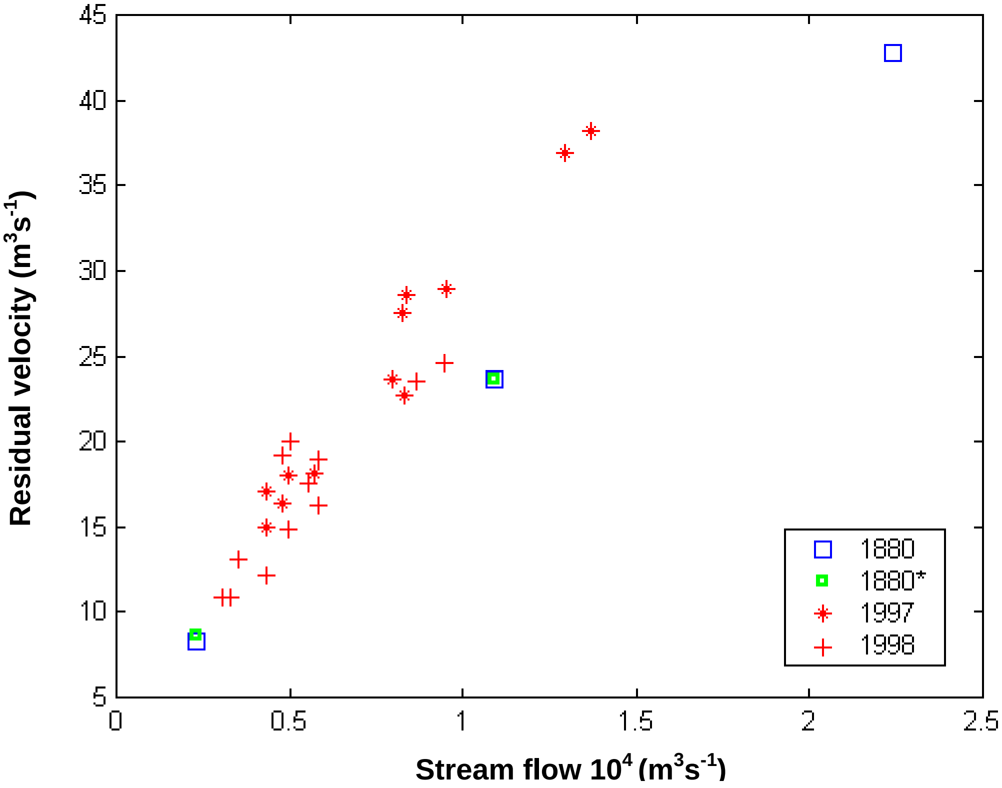


Figure 59. Residual velocities increase sharply with increasing river flow, with what appears to be a quasilinear correlation. Predevelopment and modern systems have distinguishable correlation fingerprints. For an equal river flow, the modern system has higher residual velocities than the predevelopment system, possibly because of a higher degree of canalization. Values of residual velocity shown in this figure are estuary wide, having been obtained by spatial integration of local values. Estuary-wide residual velocities show little sensitivity to controlled changes in Region 4 bathymetry (1880 vs. 1880*; see Table 9).

section (page 142), we will present evidence for life history change among juvenile Chinook salmon and assess whether changes in estuarine habitat opportunity may have contributed to these effects.

Conclusions

Numerical circulation models appear to be effective tools for identifying and characterizing physical patterns and trends in the Columbia River, and their responses to external change such as river flow. Results presented in this technical memorandum are based on a first-generation circulation model. Based on these preliminary results, we recommend the following improvements to our bathymetric database, our habitat-opportunity indicators, and the hydrodynamic model.

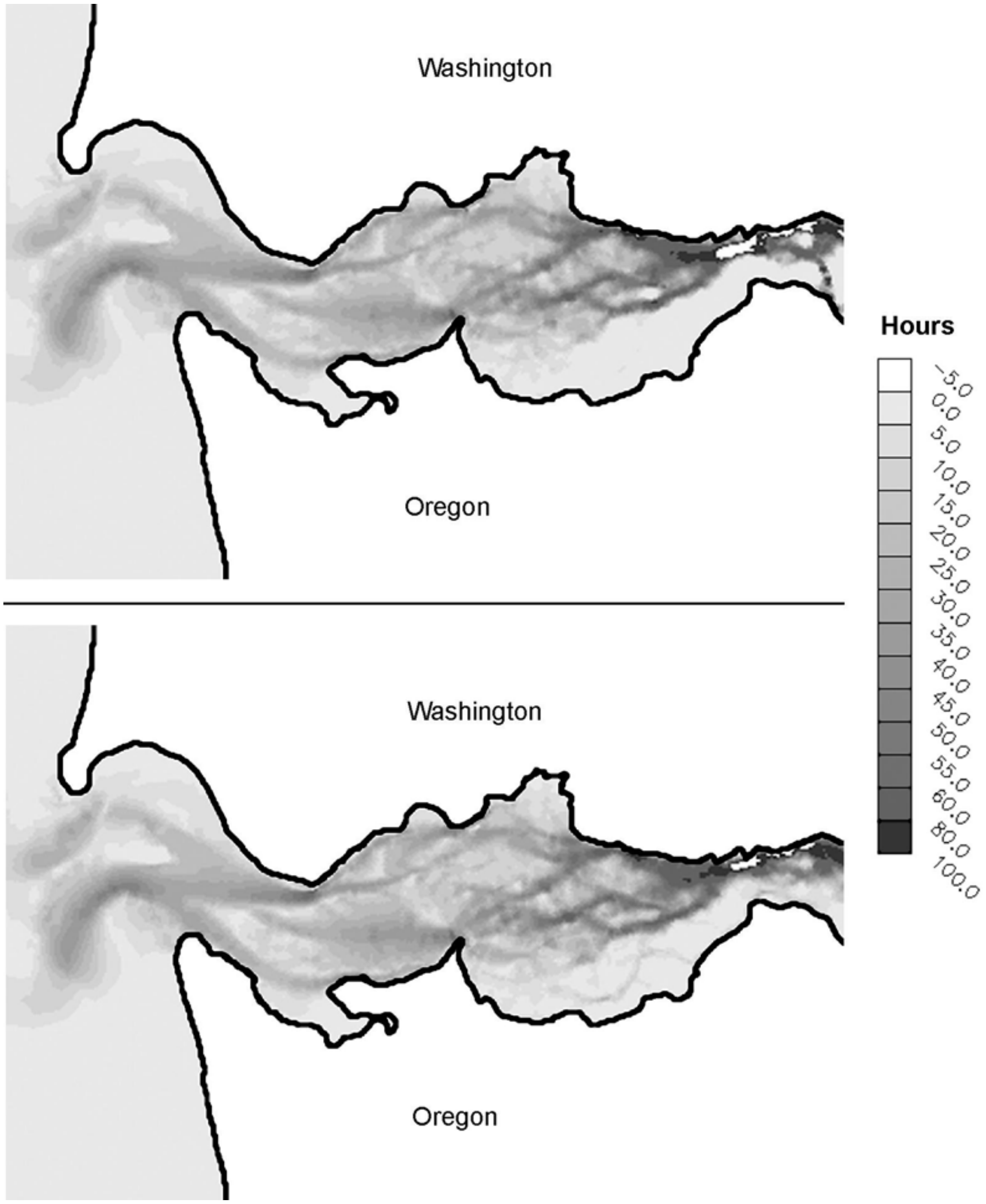


Figure 60. Reference bathymetry (top) and corrected bathymetry (bottom) for Region 4 in the Columbia River estuary for May 1880. Outside the area directly affected, residual velocities show very little sensitivity to controlled changes in the predevelopment Region 4 bathymetry. Residual velocities in Region 4 show a finer structure for the modified bathymetry, consistent with its higher degree of resolution. Results for May 1880 are online at http://www.ccalmr.ogi.edu/~ppearson/BPA/RSD1880-May.html and http://www.ccalmr.ogi.edu/~ppearson/BPA/RSD1880-Mayb.html, respectively.

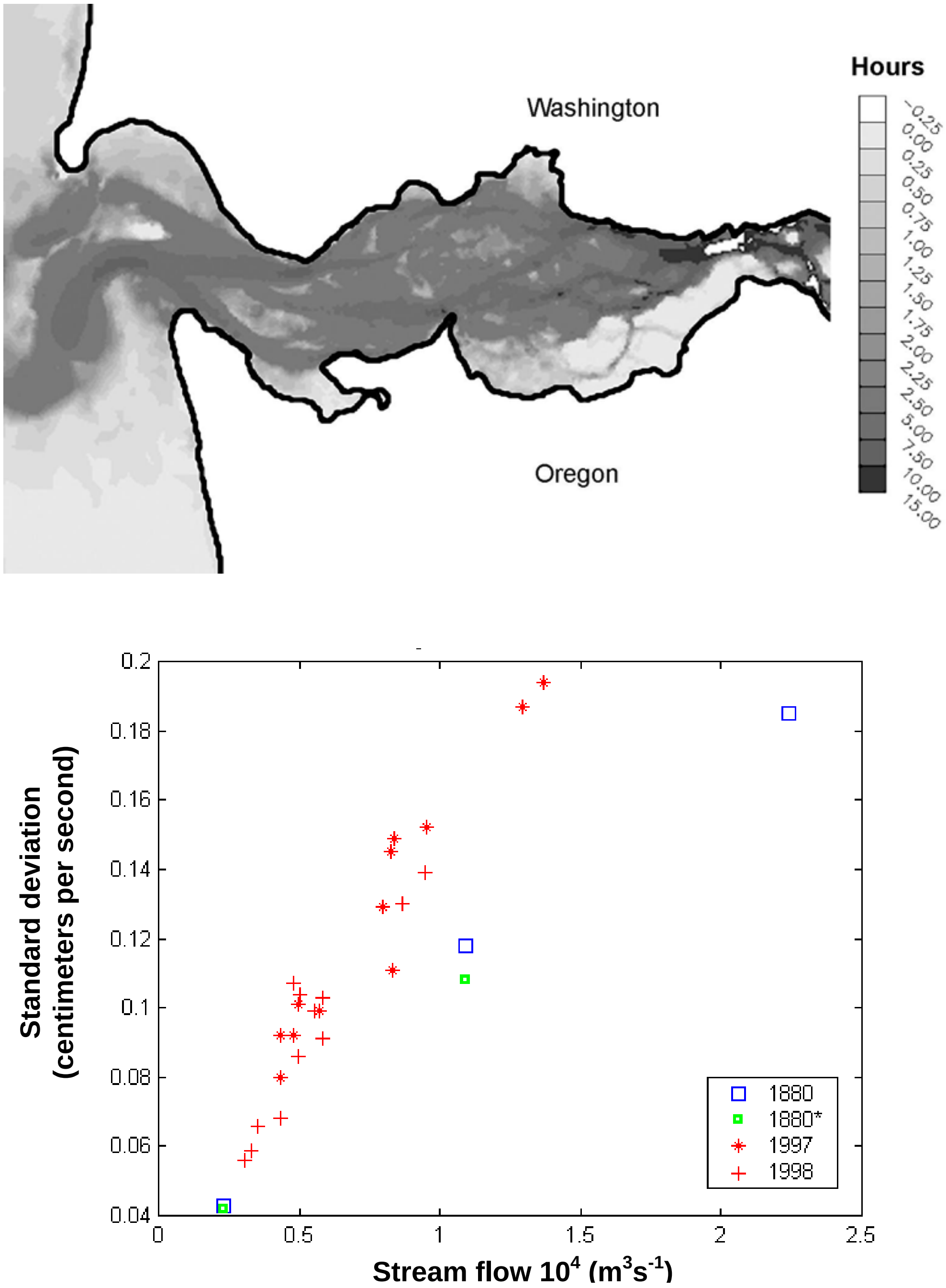


Figure 61. Variations of daily averaged residual velocities for May 1880 in isoline form (top), and estuary-wide correlation of standard deviations with flow for selected modern and predevelopment years (bottom). Patterns and trends are similar, scale aside, to those of monthly averaged residual velocities. Isoline form is online at http://www.ccalmr.ogi.edu/~ppearson/BPA/RSD1880-May.html, and standard deviations are at http://www.ccalmr.ogi.edu/bpa/figures/Resstd.gif.

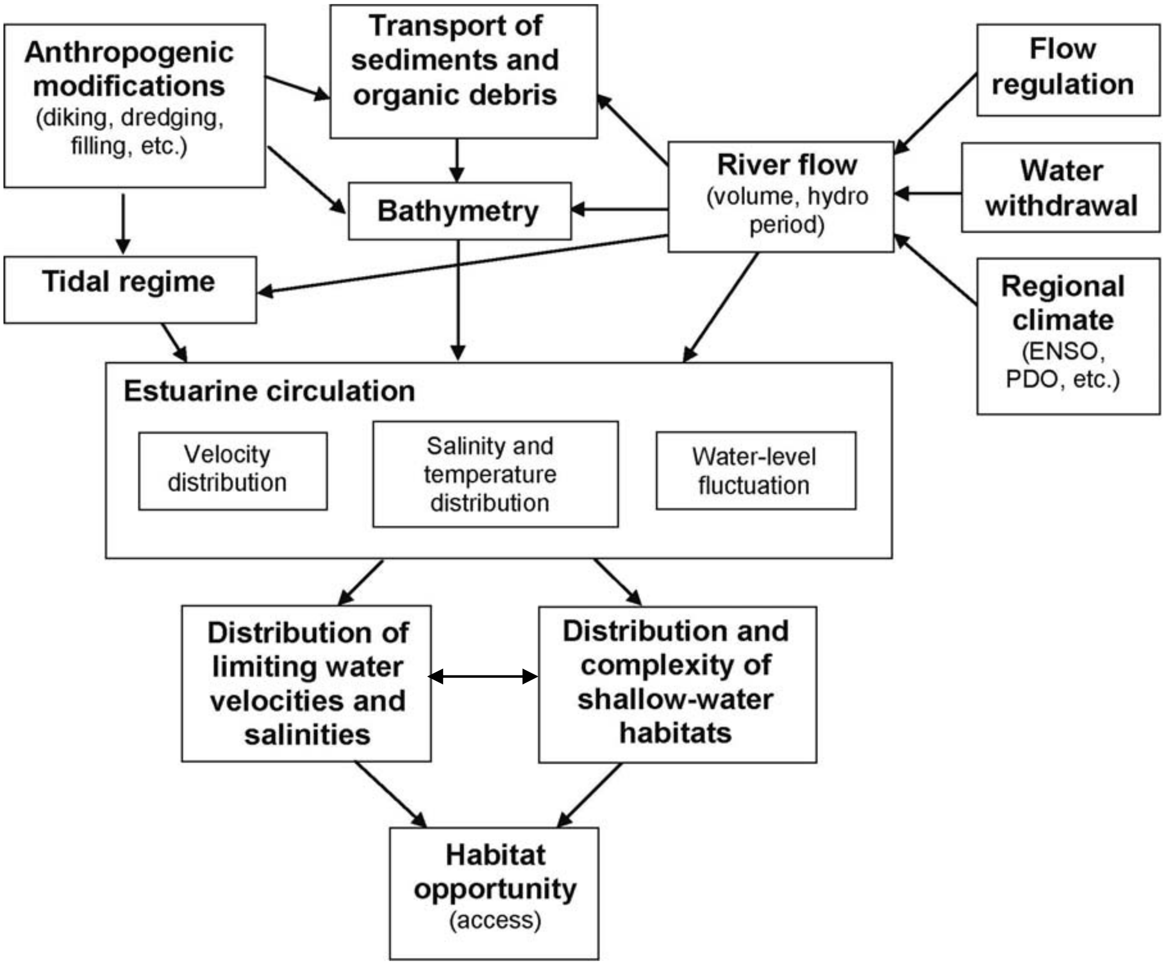


Figure 62. Conceptual model of physical linkages to estuarine habitat opportunity for subyearling salmon.

Representation of Modern Bathymetry, Particularly in the Shallowest Areas

An improved base map depicting modern bathymetry is essential to establish confidence in the model results for shallow areas. Significant improvements could be made from existing survey data and aerial photography. We recommend new bank-to-bank surveys be completed, because important shallow areas of the estuary have not been inventoried since the late 1950s. We expect that a more accurate depiction of modern bathymetry, particularly in shallow areas, would decrease our estimates of physical habitat opportunity based on depth and the combined depth and velocity criteria.

Characterizing Habitat Opportunity

Although our criteria for physical habitat opportunity have a biological basis, they have not been explicitly tested in the Columbia River estuary. Our model results indicate that the chosen threshold values for velocity and depth affect the absolute estimates of habitat opportunity more than they affect the overall trends under varying flow conditions. Salinity and temperature are key physical variables that should be incorporated in future simulations to provide a more complete characterization of salmon habitat opportunity.

Vertical structure and density effects also should be included in the model to improve representation of estuarine velocities and transport processes. A three-dimensional baroclinic circulation model for the Columbia River (Myers and Baptista 2000) is a major step toward addressing this need. The new model not only offers a more complete representation of the physics of estuarine circulation, but it is also significantly faster than the model used in this analysis. The new model will require systematic validation.

Implications for Salmonid Rearing Habitat

Despite the limitations, the model provides a new and powerful means to conceptualize habitat opportunity in the estuary and its response to physical change. In particular our results support the following interpretations:

- Habitat opportunity is strongly controlled by bathymetry and, at least in the upper estuary, river flow (Figure 48, Regions 4, 5, and 6). We did not systematically analyze tidal effects, but tides are probably another important factor controlling habitat opportunity.
- Physical relationships to habitat opportunity are distinct in different regions of the estuary. Differences appear correlated with proximity to the ocean and with the type of environment in each subregion (Figure 48). The estuarine subregions selected in this study were chosen to coincide roughly with those used in the CREDDP surveys (Simenstad et al. 1990b). In the future it may be useful to apply a finer definition of subregions based on objective criteria for bathymetry and habitat connectivity.
- Habitat opportunity varies seasonally and is often smallest during freshets. The timing of minimum habitat opportunity often reflects known shifts in the timing of freshets from predevelopment to modern times.
- The modern and predevelopment systems are distinctive in their morphology, residual circulation, and habitat opportunity.
- While it may be useful to combine two or more criteria to depict habitat opportunity, meaningful interpretation of combined results requires knowledge of relative errors and uncertainty. This is beyond the scope of this work, but it is arguably within reach of available technology.
- The velocity criterion is much less sensitive than the depth criterion to known weaknesses of the model in representing modern bathymetry (Figure 51). Differences in error and uncertainty suggest that the two criteria should not yet be combined into a single indicator of habitat opportunity.
- The most biologically relevant threshold values for the depth and velocity criteria remain uncertain (Figure 52). In future studies, an interdisciplinary analysis of physical/biological relationships is needed to develop strong indicators of estuarine habitat opportunity.

- The increased canalization of the Columbia River estuary, from predevelopment to modern times, is visible across all indices of net hydrodynamic transport. Particularly revealing are maps of spatial distribution of residual velocities (Figure 52). Moreover these effects may be significantly underestimated in this analysis, because historical and present-day floodplain, riparian, and wetland habitats are not fully represented in the bathymetric base maps used for our simulations. Effects of canalization may be greater if we also could account for widespread diking and filling of peripheral shallow-water habitats.
- There is a general level of consistency across observed trends in residual velocities and in habitat opportunity. Correlation between indices of net hydrodynamic transport and indices of physical habitat opportunity were beyond the scope of the present investigation but should be pursued in the future.
- The model predicts temporal and spatial changes in habitat opportunity that the member/vagrant hypothesis suggests could be significant to salmon diversity and resilience. Among these are changes in the timing and magnitude of river flows, increased sensitivity of upper-estuarine subregions to peak flows, and effects of increased canalization on estuarine velocities. Improved representation of historic and modern floodplain habitat in the model bathymetry is needed to better assess diking and filling effects on subyearling salmon with estuarine life histories.

Estuarine Habitat Capacity

Introduction

In the previous two sections ("Changes in Hydrological Conditions," page 47, and "Estuarine Habitat Opportunity," page 89), we emphasized the potential role of spatial processes (Sinclair 1988) in shaping salmon population diversity and dynamics in the Columbia River estuary. We examined the effects of river flow, bathymetry, and other physical influences on the total quantity and distribution of habitats potentially available to estuarine-rearing salmonids (i.e., habitat opportunity). The member/vagrant hypothesis suggests that these or other geographic factors ultimately may determine the variety of life histories that juvenile salmon can express in the estuary (see the "Conceptual Framework for Evaluating Estuarine Habitat Conditions" section, page 21). Individuals, for example, with different sizes and times of estuarine entry, residency, and ocean migration may require particular suites of habitat appropriately arrayed in time and space to support particular rearing and migration behaviors.

In addition to the physical and geographic processes that affect habitat opportunity, the member/vagrant hypothesis acknowledges that biological interactions (i.e., energetics processes)—competition, predation, or disease, for example—also may influence the performance of salmon within accessible habitats. Habitat capacity refers to various habitat qualities that can mediate biological interactions by regulating, for example, the composition and availability of prey species, the assimilation efficiency of salmon, or the ability of individuals to successfully elude predators. In this way salmon performance, as indicated by feeding success, growth, or survival, is a product of habitat opportunity and habitat capacity (Figure 63, [Simenstad and Cordell 2000]).

The factors that determine habitat capacity are not always independent or mutually exclusive. While improved water clarity, for example, increases prey detection and the reactive distance for visually feeding fish such as juvenile salmon, reduced turbidity also increases the visibility of juvenile salmon to aquatic and aerial predators. Complex ecological changes in the capacity of the estuary to support salmonids thus are difficult to quantify and cannot be simulated as readily as the physical variables that regulate habitat opportunity, such as changes in water elevation or current velocity. The assumption that food or predation in the estuary limits juvenile salmon productivity and estuarine carrying capacity has never been rigorously tested.

Furthermore, the notion of habitat capacity does not imply a single optimal condition by which salmon production is continually maximized. Just as salmon migrations and habitat opportunity vary in time and space, habitat capacity also must be understood in a broader landscape perspective. The structure of the habitat-capacity landscape, which establishes the growth and survival potential for diverse life history types and therefore the resilience of

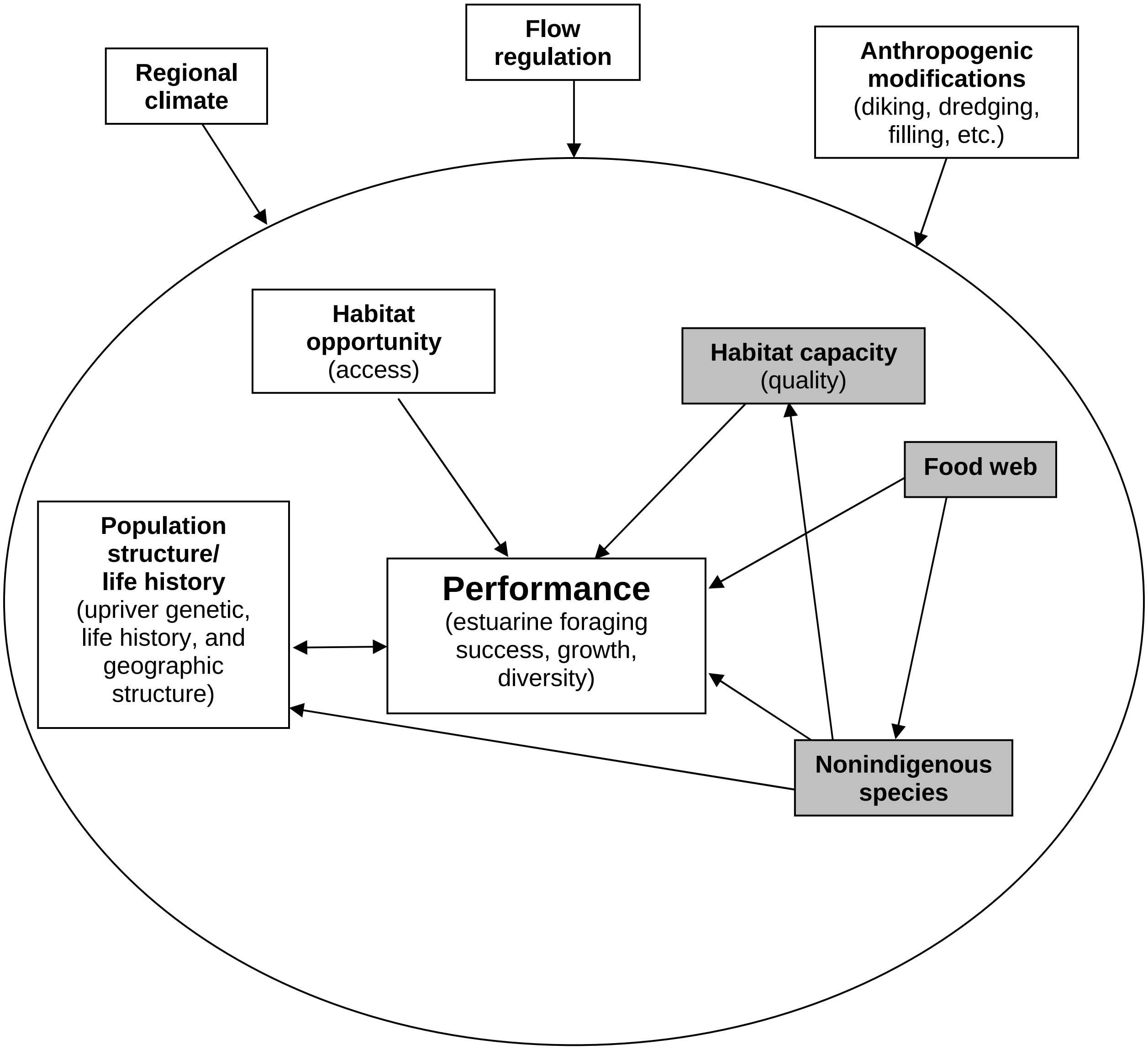


Figure 63. Habitat capacity refers to various habitat qualities that mediate biological interactions (competition, predation, etc.) and, thereby, influence salmon performance within the estuary. In this section we include altered estuarine food webs and introductions of nonindigenous species among the relevant biological factors affecting habitat capacity.

Columbia River populations, may be equally or more important than the magnitude of production.

In this section, we review what is presently known about changes in the Columbia River estuary that could influence habitat capacity for juvenile salmon, including changes in estuarine food webs, introductions of nonindigenous species, and predation effects. We then examine the implications of these changes for the member/vagrant hypothesis (see the "Conceptual Framework for Evaluating Estuarine Habitat Conditions" section, page 21).

Foraging Habitat and Food-web Changes

Substantial evidence indicates that the productive capacity of the Columbia River estuary possibly declined during the past century. Together, habitat removal by diking and filling, simplification of distributary channels, changes in detrital sources, and introductions of nonidigenious species may have disrupted food webs and other estuarine functions that historically supported juvenile salmon. However, the specific effects of such changes on salmon performance in the estuary or on adult returns to the Columbia River basin are poorly understood.

The importance of estuarine rearing to salmon recruitment has not been tested fully. In a study of one brood of native fall Chinook from the Sixes River in Oregon, Reimers (1973) demonstrated that juveniles with an extended period of estuarine rearing contributed disproportionately to the number of returning adults. Based on a series of experimental releases, however, Levings et al. (1989) found that subyearling Chinook salmon with access to the Campbell River estuary (i.e., released upstream or directly above the estuary) in British Columbia did not always (i.e., only three of four years) survive significantly better than salmon that were released directly offshore. The estuarine processes that may affect salmon survival are not well defined. Most studies have inferred that duration of estuarine residency, total growth in the estuary, and size at ocean entry are key determinants of salmon survival.

Salmonid Use of Shallow Estuarine Habitats

Ocean-type Chinook and other species and life history types (e.g., chum salmon) considered most estuarine dependent (see the “Conceptual Framework for Evaluating Estuarine Habitat Conditions,” section, page 47) rear in estuaries for up to several months. Studies in British Columbia and Washington estuaries have shown that subyearling salmon use shallow-water habitat and prey resources at least during their early stages of estuarine residency (Groot and Margolis 1991, Levy et al. 1979, Levy and Northcote 1981 and 1982, Healey 1982, and Simenstad et al. 1982). Studies in several Oregon estuaries further confirm that small, subyearling juvenile salmon typically occupy shallow habitats, including emergent marshes, forested wetlands, and peripheral floodplain channels and beaver ponds (Gray et al. 2002; Miller and Sadro 2003).

Throughout their estuarine residency, juvenile salmon consume a wide variety of prey taxa and often are described as opportunistic feeders (Healey 1991). Yet within particular estuarine regions and habitats, salmon appear to feed more selectively. In oligohaline and brackish habitats, for example, juvenile salmon feed extensively on emergent insects (particularly larvae, pupae, emergent chironomid (*Chironomidea*), and other dipteran flies, and aphids (*Apidae*) and epibenthic crustaceans (e.g., mysids [*Mysidacea*], gammarid amphipods [*Grammaridea*], [Levy and Northcote 1982, Miller and Simenstad 1997, Simenstad and Cordell 2000]). In more saline portions of the estuary, salmon often consume epibenthic crustaceans, including gammarid amphipods and harpacticoid copepods.

The diet composition of juvenile salmon that move far into shallow tidal channels and sloughs suggests that small fry and fingerlings associate with the vegetated edges of estuarine wetlands (Levy and Northcote 1982, Simenstad et al. 2000b). During low tide and reduced river flows, these fish often use shallow subtidal areas, including mud and sand flats. Principal food items of juvenile salmon in wetlands and unvegetated shallow-water habitats are the tube-dwelling benthic amphipods *Corophium* spp.

Information about habitat use and feeding ecology of juvenile salmon in the Columbia River estuary is extremely limited. Most studies on this estuary have emphasized salmon with stream-type (i.e., yearling smolt) life histories sampled in or near deep channels. Such large juveniles are less likely to rear in estuarine habitats for extended periods compared to smaller subyearling migrants. One analysis, for example, showed that the seaward migration rate of subyearling Chinook salmon decreased as individuals entered the estuary, whereas no such slowing of migration was shown for larger yearling Chinook (Bottom et al. 1984).

Existing documentation of salmonid diets in the Columbia River estuary is similarly biased toward large, stream-type fish. However, results of the Columbia River Estuary Data Development Program (CREDDP) in 1980–1981 showed that subyearling and yearling Chinook salmon in the tidal fluvial and estuarine mixing regions of the estuary preyed extensively on invertebrates from shallow-water habitats (Bottom et al. 1984, McCabe et al. 1986, Bottom and Jones 1990). *Corophium salmonis* tended to be the most prominent prey item. Other important prey species included *C. spinicorne*, unidentified insects, and opossum shrimp (*Neomysis mercedis).* Planktonic organisms were not important food items except during the summer (August) when freshwater cladocerans (*Daphnia* spp.) dominated the diet of subyearling Chinook.

Thus juvenile Chinook, coho, and steelhead showed no evidence of consuming planktonic copepods (e.g., calanoids) that are produced within the estuary. Juvenile salmon apparently select[5] *Corophium* spp. and insects from shallow-water and vegetated habitats, respectively, during the period of peak salmonid abundance in the estuary. Salmon also are supported primarily by pelagic zooplankton produced upriver, particularly in the reservoirs behind the Columbia River dams (Sherwood et al. 1990).

Effects of Wetland Loss

Losses of emergent marsh and forested wetland habitats in the Columbia River estuary have been substantial and are likely a significant factor reducing the estuary's opportunity and capacity to support juvenile salmon. Approximately 121.6 km^2 of tidal marshes (77%) and swamps (62%) that existed prior to 1870 have been lost. Together with a 12% loss of deepwater habitat, these changes reduced the estuary's tidal prism from 12% to 20% (Thomas 1983, Sherwood et al. 1990). In addition, the historic surface area of the estuary has decreased by approximately 20% as a result of diking or filling of tidal marshes and swamps.

The loss of estuarine wetlands not only reduced the total amount of shallow rearing habitat available to young salmon, but it also altered the magnitude and character of habitat capacity. The resulting decline in wetland primary production eliminated approximately 15,800 metric tons of carbon per year (mt carbon year^{-1}) or 84% of macrodetritus that historically

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[5] All inferences about habitat and prey utilization of juvenile salmon based on the 1980–1981 CREDDP sampling must be considered provisional, because that sampling design significantly underrepresented shallow-water habitats such as bays, emergent marshes, and forested wetlands that may be the location of considerable subyearling salmon.

supported estuarine food webs. This macrodetritus originated from the vascular and macrophytic plants and microscopic algae historically produced within the estuary's wetlands. However, these losses were accompanied by an increase of approximately 31,000 mt carbon year^{-1} of microdetritus from upriver sources, originating principally from increased phytoplankton production in the reservoirs behind the mainstem dams (Sherwood et al. 1990).

Absolute changes in habitat opportunity alone should not be used to directly infer changes in the capacity of the estuary to support salmon. Despite considerable loss of emergent and forested wetlands in the estuary and associated declines in macrodetrital production, for example, the total area of estuarine shallows and flats actually increased 7% between 1870 and 1980. This was independently substantiated by Sherwood et al. (1990), who estimated a 68.4×10^6 m^3 net sediment gain within the estuary between 1868 and 1958. Areas of sediment increase include peripheral bays such as Cathlamet Bay and Grays Bay, which had shoaling rates of 0.61 centimeters per year (cm year^{-1}) and 0.63 cm year^{-1}and net volumetric increases of 76.2×10^6 m^3 and 19.1×10^6 m^3, respectively. These increases have contributed to the estuary's capacity by providing some additional foraging habitat.

Shifts in the sources and types of detritus available may have altered estuarine food webs, including those leading to salmon. The epibenthic-pelagic food web, for example, supported by microdetrital sources favors production of calanoid copepods and other pelagic organisms that typically are not consumed by juvenile salmon (Bottom and Jones 1990, Sherwood et al. 1990).

Calanoid and cyclopoid copepods, however, are used by abundant forage fishes in the estuary, such as northern anchovy (*Engraulis mordax*), Pacific herring (*Clupea harengus pallasi*), and longfin smelt (*Spirinchus thaleichthys*). These species, in turn, often appear in the diets of salmon in the nearshore ocean. The survival tradeoffs between historic food webs that lead directly to subyearling salmon versus contemporary food webs that might enhance prey availability for larger outmigrants in the nearshore ocean are unknown.

The spatial distribution of the food web also may be an important determinant of habitat capacity in the estuary. Whereas the macrodetrital food web was historically distributed throughout the lower river and estuary, the contemporary microdetrital food web is concentrated within the localized mid-estuary region of the ETM.

We have no objective means to quantify the ecological effects of the habitat shift from emergent and forested wetlands to shallows and flats. No historic data, for example, are available for salmonid diet composition or stomach fullness within tidal wetlands to compare with other estuarine habitats. Although juvenile salmon may not directly benefit from the microdetrital food web, there is evidence that they have higher stomach fullness in the mid estuary compared to other estuarine regions (Bottom and Jones 1990). One possible mechanism for the increased feeding rates is that enhanced detrital concentrations within the ETM also may stimulate secondary production in adjacent midestuary shallows and flats. Yet this remains an untested hypothesis. However, we do know that prey production and salmon stomach fullness values are relatively high in protected flats compared to many estuarine habitats. Jones et al. (1990) found that the standing crop of benthic infauna in protected flats of the estuarine mixing region (≈RKm 4–RKm 11) was more than an order of magnitude higher (2.058 grams per square meter ash free dry weight [g m^{-2} AFDW]) than benthic fauna standing crop in any of the other channel or unprotected flat habitats (0.098–0.136 g m^{-2} AFDW) sampled within the same estuarine region.

Prey Availability

Another issue in assessing the estuary's capacity to support juvenile salmon is variability in the relative production and availability of prey. Fish foraging efficiency is limited by prey availability and their capacity to perceive prey. Other behavioral constraints, such as innate responses to predation cues, can also influence prey selection (Gerking 1994). In some estuaries prey resource density or distribution has been shown to limit juvenile salmonid growth (Reimers 1973). Little information is available, however, to assess the potential effects of prey resource variability on salmon in the Columbia River estuary.

High turbidities in the upper and middle reaches of the Columbia River estuary may be an important factor in fish feeding success, although historic turbidity levels likely have decreased following the construction of mainstem dams and regulation of river flows (see the "Changes in Hydrological Conditions" subsection, page 21). Contemporary evidence of turbidity effects is suggested by dietary changes among juvenile salmonids sampled at Jones Beach before and after the 18 May 1980 eruption of Mount St. Helens. Following the eruption, benthic amphipods in salmonid stomachs were supplanted by insects and cladocerans (McCabe et al. 1981, Emmett 1982, Kirn et al. 1986) suggesting that either benthic amphipods became less available or were not visible during very high turbidities. The specific impacts of these turbidity-induced changes on salmonid growth or survival are impossible to discern after the fact.

Given the fundamental lack of information on absolute growth and variability of juvenile salmon in the estuary (see the "Estuarine Growth and Residence Times" subsection, page 156), it is impossible to conclude whether the capacity of the Columbia River estuary to support salmon is limited or has significantly changed relative to historic levels. This is an important gap in our analysis because our conceptual approach (i.e., the member/vagrant hypothesis) implies in principle that spatial processes affecting habitat opportunity alone might be sufficient to explain variations in salmon production and diversity.

Nonindigenous Species

Introductions of nonindigenous species also have changed the Columbia River estuary. Weitkamp (1994) catalogued 16 exotic fish and four invertebrate species that have become established in the estuary. The unassembled list of introduced plants is undoubtedly much longer. While the number of nonindigenous plants, invertebrates, and fishes is expanding, the competitive, predatory, or other effects on juvenile salmon have not been assessed. A few prominent examples of introduced species with potentially important effects on estuarine and salmonid ecology are discussed in the following subsections.

Asian Clam

Evidence of introduction of the Asian clam (*Corbicula fluminea)* was discovered in North America in 1924, when empty shells were found in the Nanaimo River estuary in British Columbia (Britton 1979, Counts 1981, Britton and Prezant 1986). The Asian clam was first found on the banks of the Columbia River in 1938 (Burch 1944). It spread eastward into the lower midwestern and southeastern United States by the 1950s and appeared in Florida in the 1960s (McMahon 1983, Counts 1986). Tourists, fishermen, bilgewater from pleasure boats, aquarium hobbyists, migrating waterfowl, and sand and gravel mining operations are cited as vectors for spreading the clam over these long distances (Heinsohn 1958, Sinclair and Isom 1963, Abbott 1960). The economic costs of the Asian clam have been estimated at approximately $1 billion per year as a result of significant fouling of canals, culverts, and water intakes (Isom 1986, OTA 1993).

Since its appearance in the estuary in 1938, the Asian clam has expanded its distribution, including documented occurrences in the lower mainstem reservoirs and in the Willamette and tributary basins (Wentz et al. 1998). Asian clam distribution is restricted primarily to tidal freshwater regions of the Columbia River estuary, but it also extends into brackish habitats. Relatively high biomass concentrations—from 10 to 100 metric grams of carbon per square meter (mg carbon m^{-2})—have been found in protected and unprotected tidal flats, demersal slopes, and marsh and main-channel habitats. Biomass estimates as high as 10,000 mg carbon m^{-2} have been measured in subsidiary channels (Holton et al. 1984, Simenstad et al. 1984).

Despite the long history of colonization and expansion in North America, effects of the Asian clam on indigenous communities are poorly known (Strayer 1999). At high densities, Eng (1979) reported concentrations of approximately 131,000 m^{-2} in California canals), potential community-level impacts may be significant, including increased competition for space and food with indigenous species (Boozer and Mirkes 1979, Clarke 1986). In channel habitats of the Columbia River estuary, the Asian clam commonly occurs in association with important juvenile salmonid prey, including *Corophium* spp., other amphipods, and dipteran (*Ceratopogonidae*) larvae (McCabe et al. 1997, 1998). But ecological interactions among the Asian clam and salmonid prey species have not been investigated.

Under extreme conditions, high densities of the Asian clam could alter estuarine trophic structure by filtering large volumes of water (Stites et al. 1995, Thompson et al. 2003), an effect that has been hypothesized for another nonindigenous clam, *Potamocorbula amurensis*, in San Francisco Bay (Carlton et al. 1990, Kimmerer et al. 1994). Cahoon and Owen (1996), however, suggested that their experimentally measured filtering rates of 1.12–1.78 liters per day for individual Asian clams were too low to control phytoplankton biomass in a North Carolina lake. Others (Lauritsen 1986) found that the Asian clam can have a significant effect on riverine phytoplankton biomass and nutrient cycling. The influences of the Asian clam in the Columbia River estuary are not easily predicted given differences in suspended particulate matter relative to other systems where filtering effects have been evaluated.

By some measures the effects of the Asian clam may be deemed neutral or positive. For example, in some systems where it has been introduced, the Asian clam has become a common food item of fish and wildlife (Keup et al. 1963). In the Columbia River estuary, the Asian clam is recorded as prey for steelhead (Bottom and Jones 1990) and is a prominent food item for raccoon (*Procyon lotor*) and surf scoter (*Melanitta perspicillata*, [Simenstad et al. 1984]). In other systems, the Asian clam has been shown to have little or no effect on native species (Isom 1974, Fuller and Imlay 1976, Klippel and Parmalee 1979, Kraemer 1979, Taylor 1980a and

1980b) and may play a significant role in reducing turbidity and restoring submerged aquatic vegetation (Phelps 1994).

Given the ambiguity of results, the impacts of the Asian clam population in the lower Columbia River and estuary on juvenile salmon cannot be predicted from studies in other ecosystems. Research is needed for several reasons:

- to understand community interactions in the Columbia River among the Asian clam and salmonid prey species,
- to assess whether the Asian clam filters significant proportions of the sediment particulate or organic matter supplied to the estuary, and
- to assess whether the Asian clam modifies the estuary's capacity to support native species, including juvenile salmon.

Zooplankton

An introduced calanoid copepod, *Pseudodiaptomus inopinus*, also an Asian species, first appeared in the Columbia River estuary after 1980 and has since become abundant (Cordell et al. 1992, Cordell and Morrison 1996). These changes raise concerns about potential impacts on native calanoid copepods and associated estuarine food chains. *Pseudodiaptomus inopinus* overlaps spatially, although not entirely temporally, with one of the most dominant ETM zooplankters, *Eurytemora affinis*. Ironically, the status of *Eurytemora affinis* as an indigenous zooplankter in the Columbia River estuary also may be in doubt (Lee 1999).

In the Sacramento-San Joaquin Delta and San Francisco Bay, researchers hypothesize that *Pseudodiaptomus inopinus* has displaced *Eurytemora affinis* (Orsi 1995), but no such effects have been observed in the Columbia River estuary (Cordell et al. 1992, Bollens et al. 2002). During the 1980–1981 CREDDP surveys, calanoid copepods never were prominent in the diets of juvenile salmon but seasonally were the principal prey taxa among many pelagic fishes, including American shad, longfin smelt, surf smelt (*Hypomesus pretiosus*), whitebait smelt (*Allosmerus elongatus*), Pacific herring, Pacific tomcod (*Microgadus proximus*), threespine stickleback (*Gasterosteus aculeatus*), shiner perch (*Cymatogaster aggregata*), and English sole (*Pleuronectes* [*Parophrys*] *vetulus*) (Bottom and Jones 1990).

The abundance and availability of *Pseudodiaptomus inopinus* and *Eurytemora affinis* to visually feeding pelagic fishes probably are tied to advective processes that transport concentrations of zooplankton from the ETM into surface waters. Moreover, estuarine dynamics supporting particle and zooplankton trapping in the ETM have likely increased with river-flow regulation (Jay et al. 1990), suggesting that production of this zooplankton assemblage has been enhanced since at least the mid-1960s, when flow regulation became coordinated throughout the hydropower system. However, as described in the "Effects of Wetland Loss" subsection (page 130), salmon may derive few direct benefits from the increased pelagic production now concentrated in the ETM compared to the historic macrodetrital food chains that were once distributed throughout the lower estuary, including the extensive tidal-freshwater and brackish regions above the ETM.

American Shad

Among the 16 nonindigenous fishes now common in the Columbia River estuary, including common carp (*Cyprinus carpio*), banded killifish (*Fundulus diaphanus*), and yellow perch (*Perca flavescens*), only American shad, a clupeid from the Atlantic coast, have reached extraordinary abundance. Shad appeared in the Columbia as early as 1876 or 1877 after first being introduced into the Sacramento River, where they were planted in 1871 (Green 1874, Lampman 1949). In 1885 and 1886, the U.S. Fish Commission also shipped consignments of shad fry from the East Coast for release directly into the upper Columbia and Willamette rivers (Lampman 1949).

American shad are now a dominant species in the Columbia River (Wydoski and Whitney 1979). Their rapid rate of population increase generally encompasses the period since the Columbia River dams began regulating mainstem flows, with counts of fish past Bonneville Dam recorded by the U.S. Army Corps of Engineers beginning in 1949 (Figure 64). Misitano (1977) reported only one American shad larvae among monthly ichthyoplankton samples collected in 1973, but adult shad passing Bonneville Dam exceeded 1 million by the mid-1980s. Passage of adult American shad at Bonneville reached a peak of almost 3 million in the early 1990s, but it has declined progressively until a recent surge in 2001 (Figure 64).

Although American shad are now a prominent member of the lower river and estuarine ecosystem, we do not know whether they have impacted production of indigenous species. In the estuary they feed primarily on cladocerans (*Daphnia*) and secondarily on calanoid and harpacticoid copepods (*Corophium salmonis)* and the mysid *Neomysis mercedis* (Bottom and Jones 1990), indicating some overlap with juvenile salmonid diets. Shad are prey of white sturgeon (*Acipencer transmontanus*), harbor seals (*Phoca vitulina*) and marine birds, such as Caspian terns. Whether they have contributed to population increases in piscivorous predators in the estuary, and thus indirectly contributed to increased predation rates on juvenile salmon, also is unknown.

Few data exist to interpret the effects of any of these nonnative introductions on Columbia River salmon. Presumed deleterious effects on salmon are entirely speculative, because no documentation or experimental evidence exists to establish a potential interference mechanism. Despite the tremendous increases in American shad abundance, for example, we have no evidence for competitive interactions or other adverse effects on juvenile salmonids.

Given the abundance of the Asian clam and American shad and the consequences of comparable infestations in other estuaries such as the San Francisco Bay and the Sacramento and San Joaquin rivers delta, it is not unreasonable to hypothesize that their feeding activities could significantly modify, rather than enhance, the estuarine food web. The likely introduction rate of nonindigenous species through vectors such as ballast water flow can only increase under the existing practices; the recent appearance of additional nonindigenous species, such as the shrimp *Exopalaemon modestus* (Emmett 1997), can only magnify the challenges of predicting their expansion and ecological influences. However, in the absence of scientific evidence of direct competition or resource limitation, we cannot assume a deleterious effect on juvenile salmonids.

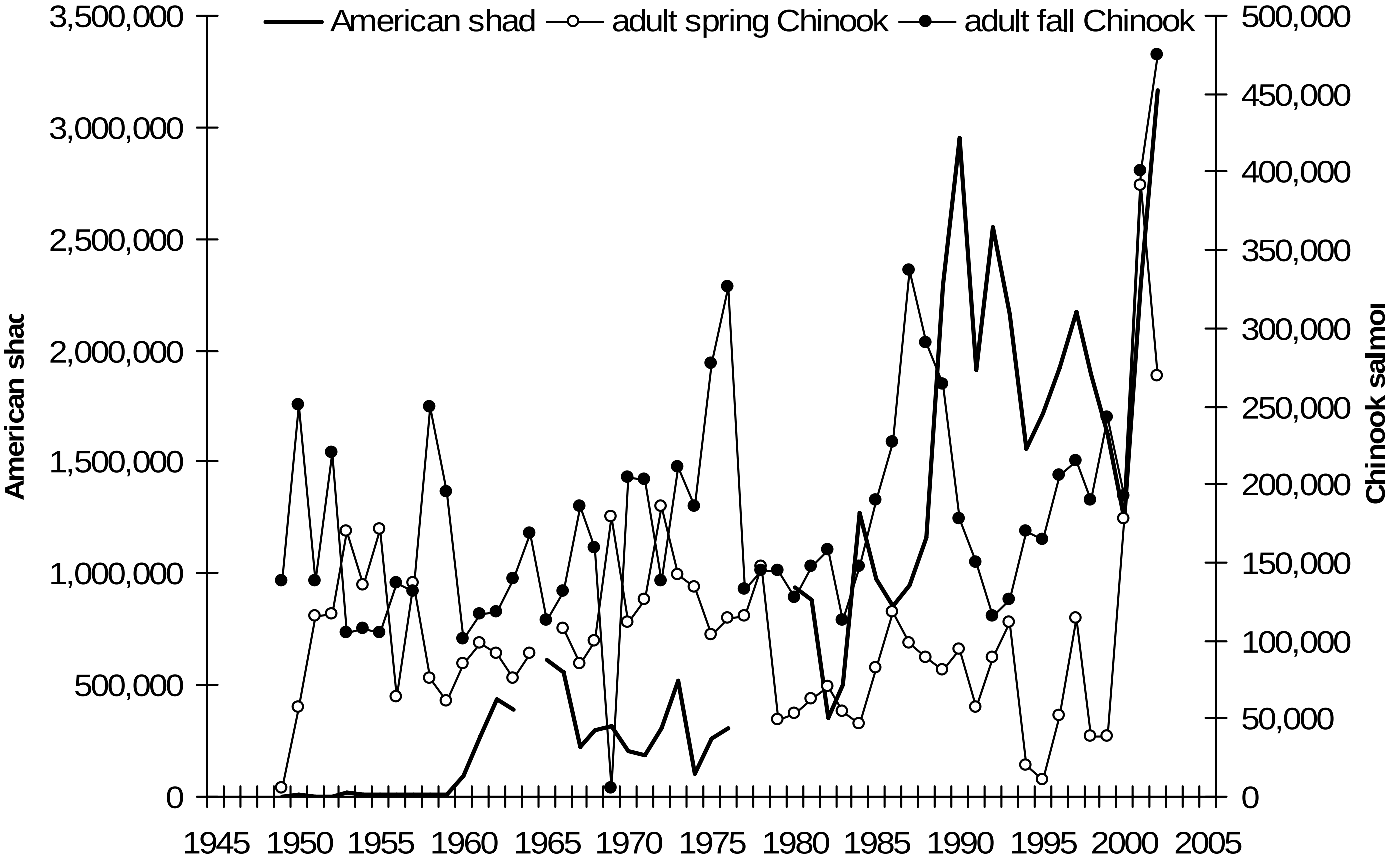

Figure 64. Counts of adult American shad and adult spring and fall Chinook salmon at Bonneville Dam, 1975–1999 (CRDART 1999). Chronology: 1885–1886, first transplants of Atlantic shad into Columbia, Willamette, and Snake rivers; 1889, commercial landings reported in Columbia; 1956, American shad pass McNary Dam; 1995, American shad spawning up to Priest Rapids Dam on the Columbia River and to Lower Granite Dam on the Snake River.

Predation

Predation on juvenile salmonids in the estuary by other fishes, marine mammals, and birds has always been a mortality factor. In many cases predation pressures may have diminished with the declines of some predator populations. Studies suggest that juvenile salmon occur infrequently in the diets of some likely predators, such as harbor seals (WDG 1984). However, several predator populations have increased significantly in recent decades, including Caspian terns and double-crested cormorants (*Phalacrocorax auritus*), which have been shown to consume significant numbers of seaward migrating juvenile salmon.

By 1999 more than 94,000 PIT tags had been retrieved from piscivorous bird colonies on artificial dredge material islands in the Columbia River estuary, representing 1.8% of the total number of PIT-tagged fish released since 1987 (USACE 1999, Good 2005). In 1998, PIT-tag codes from 15.8% of Snake River hatchery steelhead and 13.9% of Snake River wild steelhead that were either marked at Lower Granite Dam or detected at Bonneville Dam were recovered on Rice Island in the upper estuary. In the same year, tags from 2.3% and 1.3% of the hatchery and wild Snake River spring/summer Chinook salmon, respectively, were detected on Rice Island. In 1999, respective detections were 10.9% and 9.4% for hatchery and wild Snake River steelhead, and 2.3% and 1.3% for hatchery and wild Snake River spring/summer Chinook salmon (Ryan et al. 2001). Because the ratio of PIT tags deposited over water and nonnesting land sites to those deposited on nesting sites is unknown, the actual mortality rate estimates from PIT-tag recoveries is uncertain. However, estimates based on consumption rates and bioenergetic needs to maintain Caspian tern chick growth and health leads to estimates greater than 10 million seaward migrating juvenile salmon consumed in the estuary (Roby et al. 1998).

The mortality rates associated with this predation constitute a potential limiting factor on juvenile salmon survival in the lower river and estuary. Of interest are preliminary PIT-tag recoveries at Rice Island indicating that steelhead smolts were consumed in greater proportion to availability than other salmonid species, and that juvenile salmonids of hatchery origin were consumed in greater proportion to availability than wild smolts (Roby et al. 1998).

Changes in Habitat Capacity and Implications for the Member/Vagrant Hypothesis

Our results illustrate that the habitat opportunity and capacity of the Columbia River estuary may have declined through reductions in the estuarine tidal prism, surface area, and the amount of peripheral wetland habitat. Moreover, changes in the detrital sources that support estuarine food webs and increased prominence of nonindigenous species have affected competitive and predatory interactions in the estuary with uncertain, but potentially significant, consequences for salmon survival.

Yet many changes in the biological production processes of the estuary can be linked directly to physical causes (e.g., habitat opportunity). These results lend support to the member/vagrant hypothesis (see the “Conceptual Framework for Evaluating Estuarine Habitat Conditions” section, page 21), which emphasizes the role of spatial processes in shaping the dynamics and diversity of marine populations (Sinclair 1988).

The apparent shift from macrodetrital to microdetrital food chains in the estuary, for example, stems from the diking and filling of intertidal wetlands and the creation of deep reservoirs behind mainstem dams. While changes in the quality and quantity of prey resources could be a proximal factor affecting the productive capacity of the estuary, the ultimate cause is the physical removal of those vegetated habitats that supported macrodetrital production and associated epibenthic food webs.

Other biological changes in the estuary could result from nonindigenous species filling open estuarine niches or from underlying shifts in the physical conditions that have allowed these species to thrive. The population explosion by American shad (see "American Shad" subsection, page 135), for example, could reflect new habitat opportunities created for pelagic-feeding fishes with the establishment of mainstem reservoirs, the microdetrital food web, and increased trapping efficiency of the ETM. Rather than a major new competitor affecting salmonid growth or survival, American shad abundance may be a symptom of physical habitat change.

Intensive predation by Caspian terns, however, is a biological factor that may now significantly affect estuarine survival of some Columbia River salmonids. Yet one underlying cause for this apparent biological affect is the new physical habitat opportunity afforded to nesting terns when dredge-spoil islands were artificially created along the route of ocean-bound salmon smolts. Concentrated hatchery releases of stream-type salmonids, particularly steelhead, that migrate past these islands en route to the ocean possibly are another contributing factor. It becomes difficult if not impossible to separate physical from biological effects on juvenile salmon within the estuary.

We are not arguing that all biological effects are physically driven or somehow unimportant to salmon survival and abundance. We find, however, that many of the significant biological changes we now observe in the Columbia River estuary may be explained substantially by physical modifications that have altered the habitat landscape to the benefit and detriment of different species and assemblages. Habitat capacity involves a network of natural and human-induced physical changes that structure the estuarine habitat landscape, and thereby mediate many of the biological production processes leading to salmon (Figure 65). These linkages have important implications for developing restoration strategies that can address the ultimate causes rather than the proximal symptoms of salmon decline.

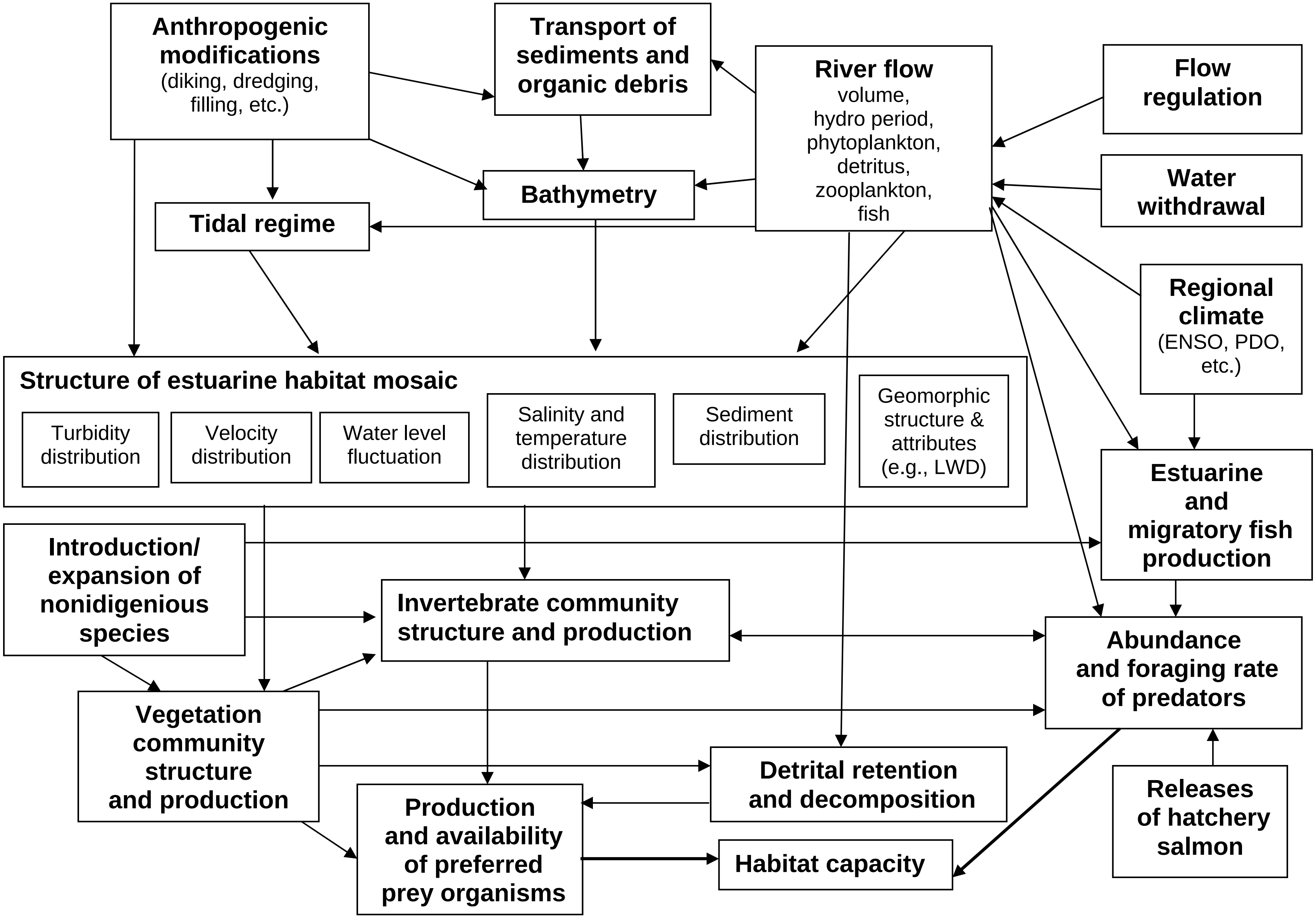

Figure 65. Network of physical and biological linkages influencing estuarine habitat capacity for subyearling salmon.

Conclusions

The most significant changes to the capacity of the Columbia River estuary to support juvenile salmon are likely the results of habitat loss. Support of the natural, macrodetritus-based estuarine food web has been significantly diminished by historical diking and filling of 121.6 km^2 of emergent marsh and tidal wetland habitat. Expansion of shallows and flats throughout the estuary, plus a reduction in the spring-freshet energy, may have compensated to an unknown degree by promoting productive shallow-water habitat. Concurrent changes to the estuary, especially increases in the abundance of nonindigenous species and predators, also may have affected the estuary's capacity to sustain juvenile salmon of diverse life history types. Yet no scientific evidence substantiates or refutes these speculations, and, regardless, many of these biological effects are also a direct expression of habitat change in the estuary.

Given the present scientific information, we draw the following conclusions:

- Habitat loss is well documented in the lower portion of estuary, but it is unknown for the tidal-fluvial region. The effects on the carrying capacity of the estuary to support salmon are unknown.
- Foraging and refuge habitat for salmon has been lost, and peripheral wetlands that are among the most critical off-channel rearing areas may have been most impacted; however, because subyearling, ocean-type salmon that utilize these habitats also appear to have declined, the estuary's rearing capacity presently may not be limiting. Nonetheless, recovery of those salmon life histories that depend on shallow-water rearing habitat will require restoration of peripheral estuarine wetlands.
- Habitat loss implies qualitative change in food-web pathways since we have no evidence to suggest that the ETM-based food-web supplants the former macrodetritus-based food web. The cumulative effects of such change on juvenile salmon remain uncertain.
- Nonindigenous species have assumed an increasingly prominent role in the estuarine biotic community and food web. Yet the impacts on juvenile salmon are speculative. Indirect effects, such as those imposed by increased filtering capacity of the Asian clam, may be the most identifiable impacts.
- We have no data to evaluate potential impacts on juvenile salmon of the well-established Asian clam population in the lower Columbia River and estuary. Understanding the significance and scale of the Asian clam effects on the estuarine ecosystem will require scientific studies of benthic community interactions among co-occurring salmonid prey species (e.g., *Corophium* spp.) and Asian clam utilization of suspended or benthic organic matter, which may be a limiting resource.
- Predation of salmon may have increased artificially, principally because of indirect enhancements of predator populations resulting from dredged material disposal practices and hatchery operations. Given that salmonids probably evolved in the presence of even higher predator populations than at present, it is unlikely that natural predation rates and temporal and spatial distributions of predators are primary limiting factors.

- A fundamental lack of information on absolute growth and variability of juvenile salmon in the estuary (see the "Change in Juvenile Salmon Life History, Growth, and Estuarine Residence" section, page 142) prevents any reliable interpretation of carrying capacity limitations at present or restored population levels. Precise estimates of growth are needed from juvenile salmon of different life history types corresponding to a range of residence times in the estuary. Approaches that utilize existing or new mark and recapture designs, as well as new techniques such as RNA/DNA analysis and the microstructure and microchemistry of otoliths to estimate estuarine residency, will be required to effectively obtain individual growth measurements.
- The most obvious biological changes in the estuary during the past century can be linked to severe modifications of physical habitat, including the diking and filling of peripheral wetlands, channelization and loss of connection with tidal floodplains, the creation of slack-water reservoirs behind mainstem dams, control of river flows and estuarine circulation, and the creation of dredge-spoil islands in the lower river. Restoration strategies intended to improve the productive capacity of the estuary for salmon or other native species must address the underlying physical causes rather than the biological symptoms of such change.

Change in Juvenile Salmon Life History, Growth, and Estuarine Residence

Introduction

The conceptual framework for this evaluation assumes that salmonid diversity, resilience, and productivity in a river basin depend on established linkages between salmon behavior and habitat. Applying Sinclair's (1988) member/vagrant hypothesis, we proposed three general mechanisms of change (spatial processes) in a river basin that can sever these linkages (Figure 9):

1) loss or degradation of physical habitat,
2) change in the geographic structure and genetic characteristics of salmon populations, or
3) changes in phenotypic behavior (e.g., artificial rearing or release strategies or flow modifications) that displace individuals from the appropriate habitat sequence in time or space necessary to retain membership in a population.

In addition to these spatial processes, our conceptual framework proposed that biological interactions (energetic processes), such as competition or predation, also may influence salmon performance within the estuary.

The previous sections provide examples of all the geographic changes that, for more than a century, have modified connections between salmon behavior and physical habitat in the estuary. Moreover significant biological changes, including altered food webs, increased abundance of introduced species, and expanded predator populations, have affected the quality of estuarine habitat for salmon (see the "Estuarine Habitat Capacity" section, page 89). Based on our conceptual framework, we predict that such changes should have diminished salmon performance (e.g., growth, foraging success, and life history diversity) in the estuary relative to historic conditions.

In this section we examine historic and contemporary data for evidence of change in the life history and performance of juvenile salmon in the Columbia River estuary (Figure 66). We use historic information to reconstruct former life histories and estuarine growth of juvenile salmon and compare these results with contemporary data. We evaluate the adequacy of available evidence to infer life history change and its potential causes, including various factors affecting population structure upriver. We also review the implications of these findings for our conceptual framework.

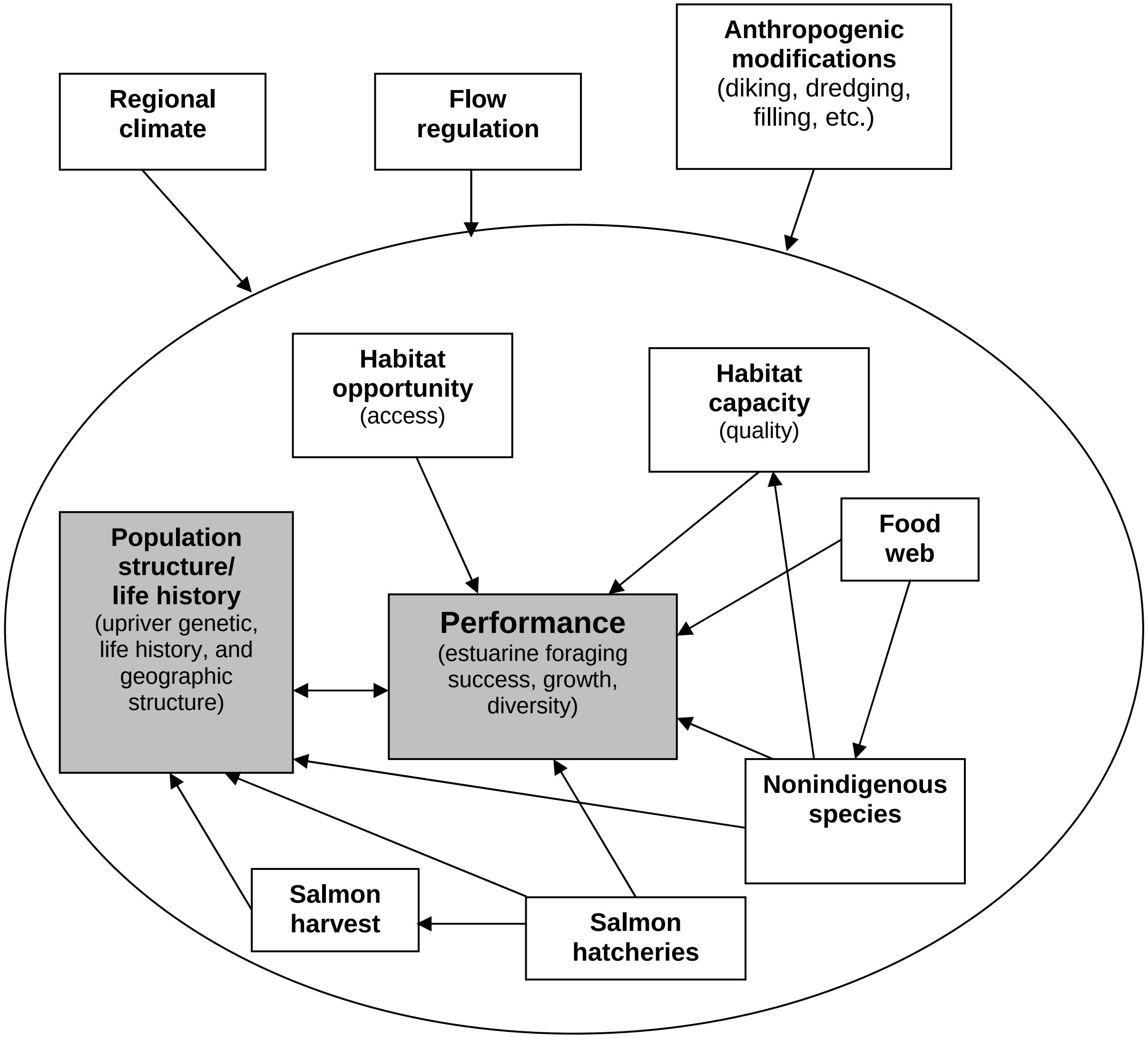

Figure 66. Together with habitat opportunity and habitat capacity, salmon performance within the estuary is directly linked to population structure upriver. To the extent that hatchery releases, salmon harvest, and watershed modifications alter population structure, they also may affect patterns of salmon rearing and migration in the estuary.

Approach and Objectives

All anadromous salmonids must pass through the Columbia River estuary en route to the ocean, and many rear there for extended periods during that transition. The patterns of estuarine use by Chinook salmon are an aggregate measure of the biological characteristics of all populations throughout the river basin and of the rearing opportunities within the estuary itself. Diversity of rearing behaviors may be apparent, for example, by the variation in sizes of individuals collected in the estuary, the times of estuarine entry, and duration of estuarine residency.

We focus our analysis of life history change on Chinook salmon for biological and practical reasons. From a biological perspective, Chinook salmon exhibit the greatest variety of rearing behaviors, and they may be the most sensitive indicators of life history change in the Columbia River basin. Because they are the most estuarine dependent of salmonid species (Healey 1982), Chinook salmon offer the best example to evaluate changes in rearing conditions of the estuary. From a practical view, there are few data available to assess effects of estuarine habitat change on other salmonid species. While information about Chinook salmon in the estuary is sparse, for most other species, it does not exist. If the data are not sufficient to evaluate effects of anthropogenic changes on estuarine rearing Chinook, we will be unable to do so for the remaining salmonid species.

Our analysis of Chinook salmon in this section is organized in three parts. We begin by reconstructing and classifying historical juvenile life histories from Rich's (1920) survey, the first detailed evaluation of Chinook salmon life histories in the Columbia River basin. These results provide a snapshot of the diversity of juvenile life histories that existed before hydropower development and other activities had substantially modified the river system. We then reanalyze Rich's data to describe historical residence times and size variations of Chinook salmon migrants upriver and in the estuary. In the third part of this section, we contrast Rich's results with modern surveys of estuarine residence times and size characteristics to evaluate potential changes in Chinook salmon life histories.

Data Sources and Methods for Life History Analysis

We reviewed published and unpublished data for wild Chinook salmon in the Columbia River basin. The principal sources we used to evaluate past and present estuarine rearing patterns are described in the following subsection.

Historical life histories and growth

Rich (1920) investigated life histories of juvenile Chinook from 1914 to 1916. During this period Rich sampled juvenile Chinook salmon throughout the estuary with a 100-foot beach seine (1.27 cm mesh in the wings and .64 cm mesh in the pocket) and to a lesser degree, by "hook and line" (Figure 67). Rich did not report catch per effort, thereby limiting our ability to estimate abundance or determine seasonal trends. He did describe, however, fork lengths (FL) of juvenile fish and analyzed scale samples to determine migration patterns and growth. We further

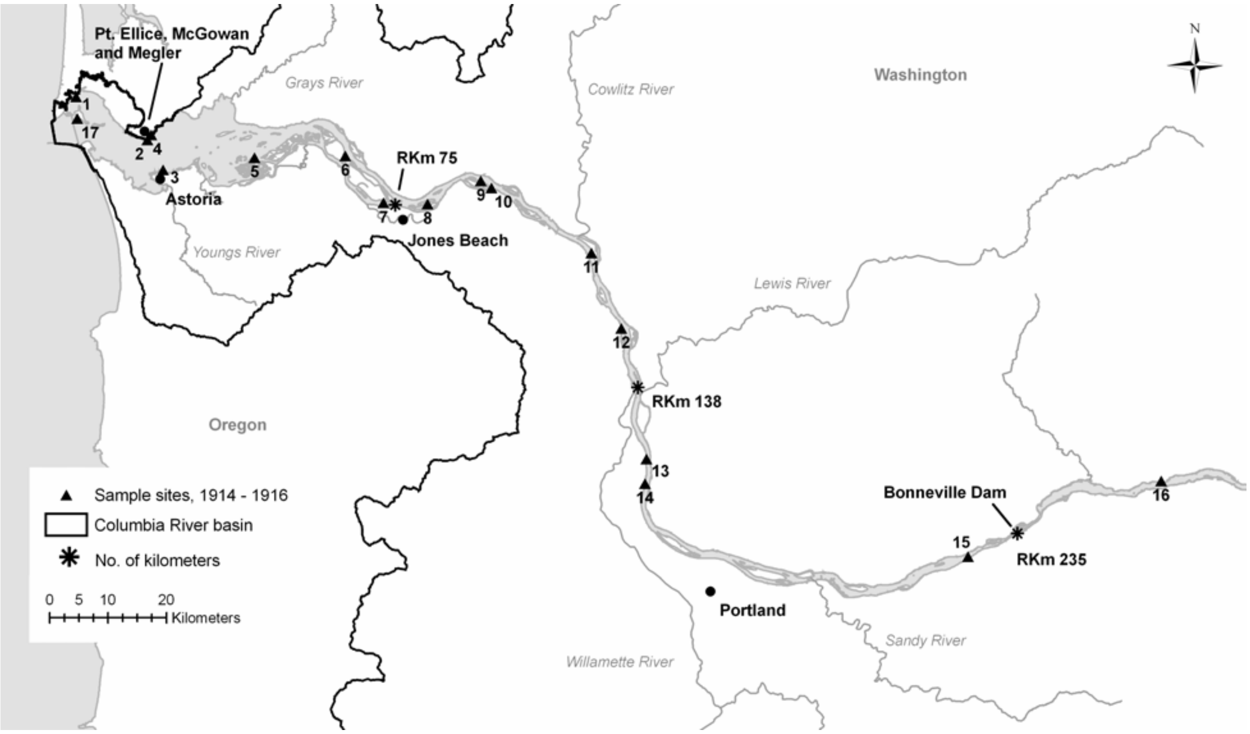

Figure 67. The Columbia River estuary and tributaries, with sites sampled by Rich (1920), 1914–1916.

analyzed his data to assess early life history attributes of subyearling Chinook salmon in the estuary, including the duration of their estuarine residency.

Gilbert (1913) was the first to recognize the relationship between scale patterns and anadromous salmon rearing behavior. Gilbert (1913) noted variations in the thickness and bandwidth of scale circuli, which indicated changes in environmental conditions. An increase in growth rate was noted by a widening of the circuli bandwidth, whereas a narrowing of the bands formed a pronounced "check" on the scales denoting slower growth rates. Gilbert (1913) and Rich (1920) identified incremental increases in circuli width that coincided with successive periods of rearing in freshwater, estuarine, and marine environments. Similar scale methodology has been used more recently to interpret juvenile rearing behaviors and their contribution to adult Chinook salmon returns in the Rogue (Schluchter and Lichatowich 1976, 1977) and Sixes (Reimers 1973) rivers in Oregon.

Rich (1920) identified and interpreted four patterns associated with check marks (narrowing of the circuli rings) on juvenile Chinook salmon scales based on the methods of Gilbert (1913):

1) no check,
2) a primary check,
3) an intermediate check, or
4) a first-year annulus.

If no check mark was observed then the juvenile had presumably reared only in its natal stream. A primary check formed when a juvenile migrated and reared in a river system downstream from its natal stream. The preceding growth was similar to the growth succeeding the check. An intermediate check indicated migration into the estuary and was associated with a notably higher growth rate compared to freshwater growth, but it was significantly less than that observed in the ocean (Gilbert 1913, Rich 1920; [Figure 68]). The beginning of a first-year annulus was first observed on scale margins of fish sampled in October and was not discernable from an intermediate or primary check because of the similar growth rates with the onset of winter (Figure 68).

Rich (1920) mathematically correlated the sizes of juveniles at the time of sampling with patterns on their scales to interpret rearing behavior, which we used to classify life history attributes. Rich analyzed the scale patterns using direct proportionality, a method developed by Dahl (1911), to back-calculate the fork length for each individual fish at various life history events denoted by checks on the scale. In the direct proportionality method, the ratio of the distance between the outermost edge of the scale and a check on the scale is proportional to the fork length at capture and the fork length at the time of formation of the mark. Rich (1920) back-calculated the size at estuary entrance for juvenile Chinook based on the fork length at capture and the distance on the scale from the outer margin to the intermediate check.

Rich's (1920) back-calculations of fish size may be subject to certain limitations associated with the direct-proportionality method. The direct-proportionality method assumes a constant relationship between growth (i.e., fork length) and scale radius. This assumption, however, may be valid since the collection occurred within one growing season (Ricker 1992).

The direct-proportionality method also is subject to Lee's Phenomenon (Ricker 1992), whereby back-calculations from larger fish tend to overestimate the growth or provide a smaller than appropriate back-calculated length when the check formed. This occurs because the method assumes the origin of the regression line for scale radius and fish fork length is zero (Ricker 1992), when in fact scales develop when juvenile Chinook salmon are about 30–40 mm (Rich 1920). Thus the slope of the relationship between scale radius and fork length is less than direct proportionality estimates. Rich (1920) unfortunately reported his results as averages for each size class (5 mm), which leaves no record of variability in scale circuli counts, scale radii, or back-calculated fork lengths within each size class and no possibility of adjusting the back-calculated values. The analyses and results we present, therefore, may be mathematically biased, particularly for the larger juveniles. Our life history classifications and relative fish comparisons, however, should not be affected by the bias.

Because Rich (1920) rarely sampled each site more than once during the three years of his survey, we cannot compare trends in population abundance, size, or life history characteristics throughout the estuary. However, he collected a consistent series of samples from 31 March to 26 August 1916 at Point Ellice, a Washington site 19 RKm upstream (Figure 67 and Figure 69). These data provide a comparative time series of Chinook life history attributes during the summer and early fall. Rich (1920) combined two beach seine sets in May, one from Tenasillihee Island in Oregon, approximately 38 RKm upstream, with those from Point Ellice, since he observed no significant differences in scale patterns between the sites. We used Rich's (1920) back-calculations of fish size to estimate the total growth from estuary entrance until their

Figure 68. Example of subyearling Chinook salmon scale patterns analyzed by Rich (1920). Both scales were collected at Point Ellice on 16 October 1915. Scale on the left depicts natal stream growth rings, an intermediate check mark, and estuarine growth (starting at A) on the outer margin. Scale on the right depicts a fall migrant with riverine rearing (starting at B) and the start of winter band on the outer margin (reprinted from Rich 1920).

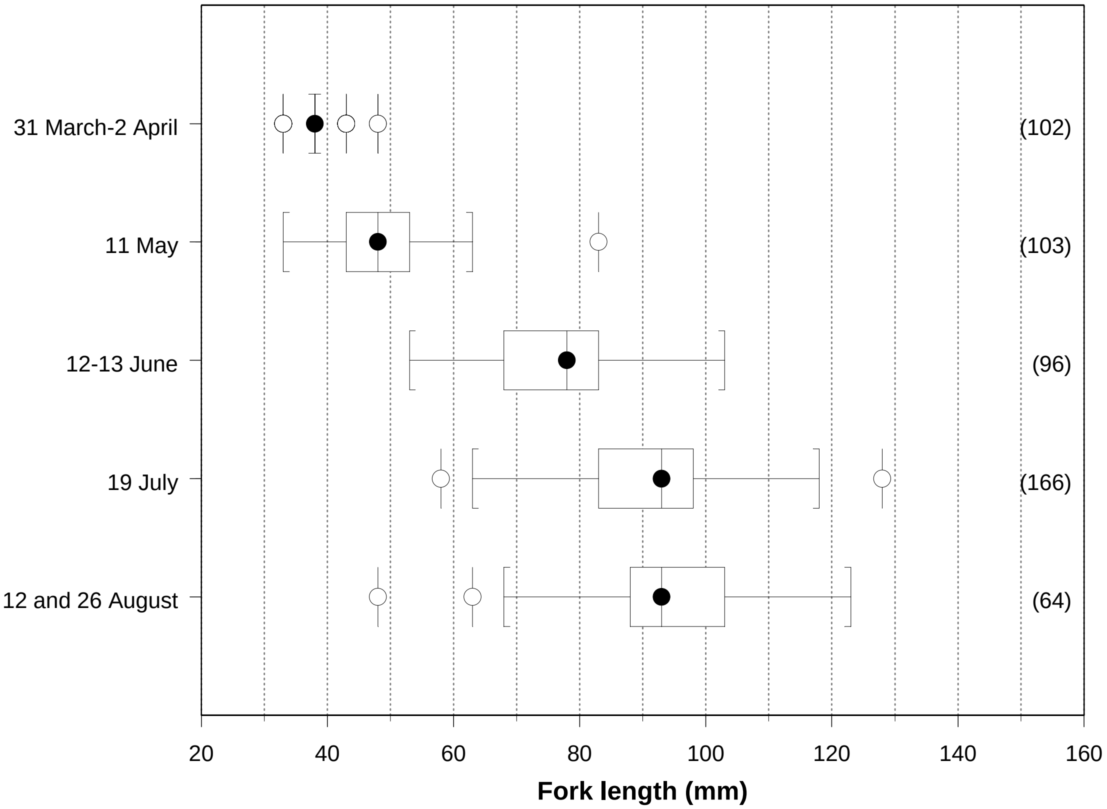

Figure 69. Range of subyearling Chinook salmon fork lengths collected by Rich (1920) at Point Ellice, March–August 1916 (31 March collection in Oregon included samples from Mayger, Sand Island, and Grims Island). Data are presented in quartiles with boxes representing 25th and 75th percentiles, whiskers extend to1.5 multiplied by the interquartile range, median is solid circle, all outliers are hollow circles, and number in collection is in parentheses.

capture at Point Ellice. We also applied a conservative estimate for estuarine growth rates of Chinook salmon based on literature values to estimate residence times for juveniles collected at Point Ellice. We also examined the size structure of the subyearling Chinook population in the collection. Although clearly not representative of all habitats or salmon life histories in the estuary, the Point Ellice results provide the only consistent data series for interpreting sizes at estuary entrance or growth rates of juvenile Chinook before substantial alterations occurred throughout the Columbia River basin and the estuary.

Contemporary life histories and size characteristics

We know of no contemporary estuarine surveys or scale analyses of wild Chinook salmon directly comparable to Rich (1920). Consequently we cannot quantitatively assess changes in estuarine life histories and residency of Chinook salmon since 1916. No contemporary growth rates for salmon exist for the Columbia River estuary. Several surveys in the estuary and in tributary streams allow us to qualitatively compare historical and contemporary life history attributes and size structure. Reimers and Loeffel (1967) reported the timing and duration of migration into the estuary from 11 tributaries of the lower Columbia River, from which we extracted examples of the diverse migration patterns of wild juveniles within a subbasin. McIsaac (1990) compared migration timing and adult contribution between wild and hatchery-reared subyearling Chinook salmon in the Lewis River in Washington. We further analyzed the Lewis River data to describe recent abundance patterns and timing of salmon migrations to the estuary.

To compare recent size characteristics of juvenile salmon to the results of Rich (1920), we analyzed a variety of published and unpublished records from miscellaneous surveys conducted near Point Ellice. The most comparable data were from Dawley et al. (1986) and Dawley[6], who used similar gear and sampled habitat similar to Rich during a 1966 beach-seine survey at Megler, approximately 1.5 RKm downstream from Point Ellice. Dawley et al. (1986) used a 95 m beach seine with variable mesh in the wings (1.27–1.9 cm mesh) and 0.64 cm mesh in the pocket. Because hatchery fish were not marked in the 1960s, we were unable to separate wild from hatchery subyearlings in these records.

More recent surveys comparable to Rich (1920) were conducted as part of the CREDDP, a comprehensive ecological survey of the estuary below Puget Island, 75 RKm upstream. NMFS biologists inventoried fish assemblages monthly using a variety of gear types at 63 stations from January 1980 to July 1981. Analyses of salmonid catches during the NMFS surveys were presented in Durkin (1982), Bottom et al. (1984), and McCabe et al. (1986). We analyzed size characteristics of juvenile Chinook from unpublished purse seine and trawl data collected in the north channel (18.9–19.4 RKm) during CREDDP and additional 1980 purse-seine data collected at McGowan, Washington (16 RKm) and reported in Dawley et al. (1985). In contrast to the 1966 survey data, a proportion of the fish released from Columbia River hatcheries during the more recent surveys were marked so that some of the hatchery fish are identifiable in the data. Unmarked Chinook salmon, however, represent a mixture of hatchery and wild juveniles.

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[6] Earl Dawley, NMFS Point Adams Field Station, Hammond, Oregon. Pers. commun., March 2000.

Most of the present-day information about the estuarine life history and movements of Chinook salmon is derived from migration rate and survival studies of marked hatchery fish. NMFS biologists have been monitoring Chinook salmon at Jones Beach from 1966 to 1972, 1977 to 1983, and 1995 to the present (Dawley et al. 1986, Ledgerwood et al. 1997). We selected tag groups of hatchery fish collected during the Jones Beach surveys prior to 1983 to analyze population size structure, timing, and abundance of migrant hatchery Chinook salmon. Salmon were collected at Jones Beach primarily by beach and purse seine, with subyearling salmon concentrated in the beach seine collections (Dawley et al. 1986). Approximately 2.3–6.5% of all fish recovered at Jones Beach were tagged or fin clipped. The vast majority of the marked fish had coded-wire tags bearing numbers unique to a particular hatchery or study. This marking method is used to track groups of fish but not individuals. More than 90% of these marked fish were hatchery-reared juveniles. The remaining unmarked fish (93.5–97.7%) were of either wild or hatchery origin (Dawley et al. 1986).

Life History Reconstruction

Our interpretation and classification of Rich's (1920) historical survey of juvenile Chinook salmon and their scale patterns revealed evidence of at least five forms of ocean-type juveniles (Table 10) in addition to stream-type juveniles. The characteristics of each stream- and ocean-type life history interpreted from Rich (1920) are described in the following subsections.

Stream-type Juveniles

Stream-type juvenile Chinook salmon migrate to the ocean as yearlings (age 1) and were present in late March to early May estuary samples. Fork lengths of yearling fish ranged from 81–125 mm. Rich (1920), however, was confident that most yearlings left the estuary for the ocean by June since they were absent in all subsequent samples.

Ocean-type Juveniles

Ocean-type juvenile Chinook salmon, which migrate to sea during their first year, vary considerably in their early life histories. During Rich's (1920) surveys, ocean-type juveniles were substantially more abundant than stream-type juveniles in all samples where both were present (Figure 70). Rich grouped the juveniles according to the presence and absence of scale marks and discussed the mechanisms responsible for the observed differences. We further classified ocean-type juveniles into a series of subgroups based on their size, rearing behavior, and seasonal time of capture in the estuary (Table 10). Since the data from Rich are inadequate to conclude the time at which the juveniles entered the ocean, the following interpretations of ocean-type life histories are presented as hypotheses.

Fry

Chinook salmon fry (defined in this analysis as fish < 60 mm FL) arrived in the estuary over an extended period and were distributed throughout tidewater. Fry were consistently collected in the marine, brackish, tidal-riverine regions of the estuary from late March through September 1916, and in December 1915 (Figure 67, Table 11). Fry less than 50 mm FL comprised 25% of all the juveniles Rich (1920) sampled in the Columbia River estuary.

Table 10. Interpretation of subyearling Chinook life history from scale analyses (Rich 1920).

Scale structure	Life history type collected	Rearing behavior	Percent of total
No check marks	Fry	Short rearing period in natal stream	33
No check marks	Fingerling smolts and recent arrivals	Reared in natal system. Migrated immediately as a fry to riverine system following emergence.	28
Primary check only	Fingerling adfluvial rearing	Natal-rearing as fry. Riverine rearing as fingerling.	6
Intermediate check only	Fingerling estuarine rearing	Began rearing in estuary as fry. Natal-rearing followed by estuarine rearing.	25
Primary and intermediate checks present	Fingerling riverine and estuarine rearing	Riverine rearing succeeded by estuarine rearing. Indistinguishable from primary and annulus combination if intermediate check formed in early winter.	8

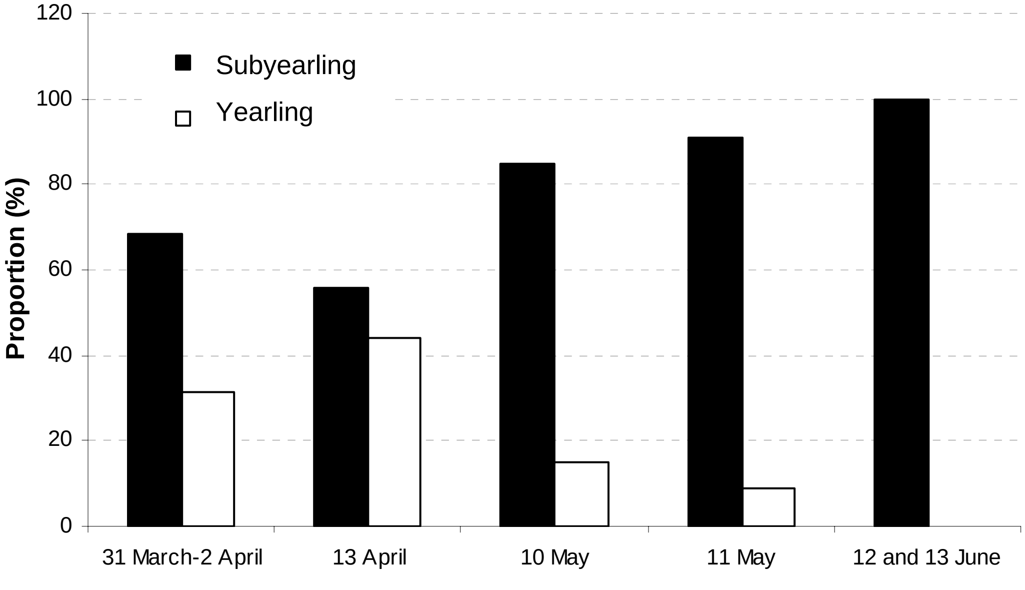

Figure 70. Proportion of subyearling and yearling Chinook salmon collected concurrently in 1916 (Rich 1920). Yearling Chinook salmon did not appear in samples after May.

Table 11. Attributes of fry collected in the Columbia River estuary by Rich (1920).

Attributes	**3 Dec 1915**	**31 Mar–Apr 1916**	**13 Apr 1916**	**10 May 1916**	**11 May 1916**	**25 May 1916**	**12–13 Jun 1916**	**19 Jul 1916**	**12 & 26 Aug 1916**	**15 Sep 1916**
Site[*]	5, 8, 10, 12, 13, 14	1, 2, 9, 10	11, 12	7, 9	1, 2	4	2	2	2	9
Brackish or tidal-riverine (TR)	TR	TR and brackish	TR	TR	TR and brackish	Freshwater	Brackish	Brackish	Brackish	TR
FL range (mm)	35.5	31–50	31–60	31–60	32–60	36–60	51–60	56–60	46–50	56–60
Fry less than 50 mm (%)	100	100	88	69	73	75	–	–	100	–
Number of fry smaller than 60 mm	1	102	24	166	100	23	7	1	1	1
Percentage of collection less than 60 mm	6	100	92	76	97	96	9	2	4	2
Number of circuli formed (fry < 60 mm)	–	2–3	2–5	1–6	2–6	2–7	4–7	9	4	13
Number of migrants smaller than 70 mm	1	102	26	191	102	25	26	6	4	22

[*] The site numbers correspond to the site numbers in Figure 67.

Fry collected in the estuary were as small as 31 mm FL. All subyearling fish collected from 31 March to 2 April 1916 were less than 50 mm FL range (n = 102). Most of these fish were collected at Sand Island (≈7 RKm) and Point Ellice (≈19 RKm). Almost half (45%) of the fry in this sample showed evidence of riverine or estuarine growth on their scales. Successive fry collections are described in Table 11. August and September samples confirmed a late fry migration into the estuary. Several smaller subyearlings in the 40–70 mm FL range were found in brackish waters at Point Ellice in mid-August and in the tidal-riverine region as late as September (Table 11).

Rich (1920) contended that the recent arrivals less than 60 mm might have originated from stream systems with conditions that produced relatively low growth rates. Alternatively, the fry may have originated from upper Columbia River tributary streams that coincided with a later emergence time. The possibility of later emergence times was supported by more recent studies in the Lewis River, which provided evidence that salmon fry continued to emerge from the gravel for at least a 3.5-month period (April–August; [Reimers and Loeffel 1967, McIsaac 1990]). While the number of fry arriving in the fall is extremely small, the data indicated a large range in the emergence times and that at least some fry arrived in the estuary late in the season.

Fry that did not rear in the lower estuary for an extended period may have headed directly seaward. The presence and survival of individuals of this life history type were supported by typical ocean-type scales with the juveniles arriving in the ocean as small fry, which Rich and Holmes (1928) found among returning adults sampled in 1923–1924.

Fingerlings

Subyearling Chinook salmon greater than 60 mm FL (fingerlings) were present at lower and middle estuary sampling sites from April to December 1916. Fingerlings first appeared in samples collected on 13 April and 11 May in the upper estuary, although they were less abundant than fry. The collection of 12–13 June showed an increase in fingerling abundance in the middle estuary.

There are four distinct types of fingerling life histories identified from the scale patterns documented by Rich (1920).

Recent arrivals—Rich (1920) interpreted scales without checks as subyearlings that had recently migrated to the estuary and had not yet had an opportunity to feed after leaving their natal stream. Approximately 63% of the fingerlings collected had scales that did not possess check marks. Without specific data from Rich (1920), we must assume that the recent arrivals could have included smolts headed seaward and fingerlings bound for estuarine rearing habitats.

Estuarine rearing—Fingerlings with only an intermediate scale check (14% of total collection) had reared for a short period in their natal stream and migrated to the estuary to rear. Fingerlings of this type, which were present in the estuary from June through September, arrived as either fry or fingerlings. For instance, subyearlings collected from June to August 1916 at Point Ellice ranged from 61 to 130 mm FL and, based on back-calculations from scale measurements, had arrived in the estuary at 38–80.5 mm FL. All subyearlings with evidence of estuarine growth were greater than 60 mm FL at capture and were on average larger than those lacking estuarine growth in the same collection (Table 12). The proportion of subyearlings with evidence of estuarine growth varied by month, but peaked at 70% in the mid-July sample. The fork length at arrival in the estuary was highly variable between sample sites and months. An unusual collection in September 1914 at Ilwaco, Washington, under a cannery yielded subyearlings that had entered the estuary at 70–118 mm FL. Rich (1920) found that these large fish fed exclusively on the discarded offal and may have delayed ocean entry due to optimum feeding opportunities.

Riverine rearing—Rich (1920) defined fingerlings with only a primary scale check as individuals that had migrated to a lower, larger stream system (riverine system) early in their life history, forming the primary check. Fingerlings with only a primary check were first collected in the estuary in October 1914. They constituted 26% of the total 332 fingerlings collected from October to November 1914 and from October to December 1915.

All subyearlings of this life history type were 95–150 mm FL. The primary check formed when individuals were 40.5–88 mm FL, indicating that some of the juveniles had migrated to a lower stream system as fry, while the others had remained to rear in the natal stream for an extended period prior to seaward outmigration. The amount of riverine growth was equal to or greater than their natal-stream growth, based on the length of the anterior scale radius. The lack of widening of the bands, however, precluded classification as estuarine growth. The primary check, therefore, indicated that the subyearlings had migrated from their natal stream to rear in a larger stream system before arriving in the estuary.

Riverine rearing with an additional check mark—Fall samples (October–December 1914 and 1915) were composed of larger subyearlings (90–205 mm FL) with two check marks signifying that they had reared for a short period in the riverine, and potentially, the estuarine environment (second mark) or formed a first-year annulus. Primary or intermediate checks that formed in the late fall and winter were not distinguishable from annuli. Rich (1920) classified the outermost check regardless of what point in the fish's life history that the mark formed as intermediate, but he recognized that it may have been an annulus. These fingerlings had migrated to a larger stream system (forming the primary check) and had either reared in the estuary (forming an intermediate check) or laid down an annulus in the river or the estuary. The primary checks were formed at 38–88 mm FL, the majority of which were fry indicating formation early in their life history. The subyearlings with both scale checks averaged about the same fork length or were larger than the subyearlings without the second check in the same collection. The estimated fork length at which the intermediate check formed on all the fish was within the last 30 mm of total growth, which means the placement of the intermediate check was relatively recent and does not eliminate the possibility that it was an annulus. All intermediate checks formed in late fall were likely annuli so that subsequent growth on the scales represented second-year growth rather than estuarine growth.

Table 12. Sampling effort and juvenile Chinook salmon attributes interpreted from scale patterns, 1914–1916. (The second part of this table on page 155 is a horizontal, right-hand continuation of the first page.)

							No circuli marks			
Type and Date	**Site***	**Gear type**	**Number of fish**	**Number of fish ≤60 mm**	**Number of fish >60 mm**	**Percent of sample with estuarine growth**	**Number of fish**	**Percent of sample**	**FL range (mm)**	**Mean FL (mm)**
Subyearling										
17 September 1914	1	Hook and line	35	–	35	80	7	20	116–120	118
24–27 October 1914	1	Beach seine	100	–	100	94	3	3	121–125	123
7 November 1914	3	Hook and line	6	–	6	100	–			
16 October 1915	2	Beach seine	119	–	119	24	30	25	96–125	113
17 October 1915	3	Hook and line	61	–	61	70	7	11	106–155	125
19 November 1915	15	Beach seine	7	–	7		6	86	91–95	93
3–8 December 1915	5,8,10, 12,13,14	Beach seine	39	1	38	54	18	44	31–95	93
31 March–2 April 1916	1, 2, 9, 10	Beach seine	102	102	–		102	100	31–50	39
13 April 1916	11,12	Beach seine	26	24	2		26	100	31–70	43.2
10 May 1916	7, 9	Beach seine	218	166	52		218	100	31–100	52.7
11 May 1916	1, 2	Beach seine	103	100	3		103	100	31–85	46.8
13 June 1916	4	Beach seine	36	33	3		36	100	36–70	47.7
12–13 June 1916	2	Beach seine	96	7	89	17	80	83	51–105	75.7
19 July 1916	2	Beach seine	166	1	165	70	50	30	56–115	89.9
12 & 26 August 1916	2	Beach seine	64	1	63	58	27	42	46–110	87.8
15 September 1916	9	Beach seine	69	1	68	4	66	96	56–90	74
Totals			**1,247**	**436**	**811**		**779**			
Yearling										
31 March–2 April 1916	1, 2, 9, 10	Beach Seine	47			72	–			
13 April 1916	11, 12	Beach Seine	22			77	–			
10 May 1916	9	Beach Seine	39			100	–			
11 May 1916	2, 6	Beach Seine	10			100	–			
Subtotals			118				–			
Totals			**1,365**				**779**			

* The site numbers correspond to the site numbers in Figure 67.

Table 12 continued. Sampling effort and juvenile Chinook salmon attributes interpreted from scale patterns, 1914–1916. (This page is a right-hand, horizontal continuation of page 154.)

	Primary check only (without estuarine growth)				Estuarine growth (second year growth by October)										
						Primary check			Fork length			Growth			
Type and date	Number of fish	Percent of sample	FL range at onset (mm)	Riverine growth (%)	Number of fish	Number of fish	FL range at onset (mm)	Riverine growth (%)	Range (mm)	Mean (mm)	Range at onset (mm)	Range (mm)	Mean (mm)	Range (%)	Mean (%)
Subyearling															
17 September 1914	–	–	–	–	28	–	–	–	101–155	123.5	70–118	15–55	30.4	11.3–35.9	23.6
24–27 October 1914	3	100	49.7	60	94	36	38–88	–	106–205	148.3	88–123	20–83	48.1	16.9–42.7	29.9
7 November 1914	–	–	–	–	6	5	48.8	–	131–135	133	111.6	21.4	21.4	16.1	16.1
16 October 1915	60	67	47.1–88.0	40.5–60.5	29	17	43–5	–	96–135	112.1	86–118	10–30	17.9	7.8–24.4	15.5
17 October 1915	11	30	40.5–65.5	42.0–67.1	43	33	43–63	–	96–180	130.9	78–123	5–60	27.0	5.1–33.7	19.6
19 November 1915	1	14	No data	No data	–	–	–	–	–	–	–	–	–	–	–
3–8 December 1915	–	–	–	–	21	–	–	–	76–130	91.5	63–98	10–35	22.0	12.8–27.3	22.0
31 Mar–2 Apr 1916	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
13 April 1916	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
10 May 1916	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
11 May 1916	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
13 June 1916	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
12–13 June 1916	–	–	–	–	16	–	–	–	66–95	83	49–63	20–38	27.7	28.7–43.6	34.1
19 July 1916	–	–	–	–	116	–	–	–	61–130	93.3	38–77	13–85	40.0	19.8–66.4	41.5
12 & 26 Aug 1916	–	–	–	–	37	–	–	–	76–125	98.4	48–81	30–50	40.6	31.8–52.6	40.6
15 September 1916	–	–	–	–	3	–	–	–	86–90	88	39–39	49–49	48.7	55.3	55.3
Totals	**75**				**393**	**91**									
Yearling															
31 Mar–2 Apr 1916	–	–	–	–	34	4	–	–	86–115	96.4	70–86	19–28	22.5	19.5–27.2	22.5
13 April 1916	–	–	–	–	17	–	–	–	106–110	108	87.2	20.8	21.8	19.3	19.3
10 May 1916	–	–	–	–	39	–	–	–	81–125	103	53–101	22–43	28.8	18.3–36.8	28.2
11 May 1916	–	–	–	–	10	3	–	–	106–110	108	73.7	34.3	34.3	31.8	31.8
Subtotals	**0**				**100**	**7**									
Totals	**75**				**493**	**98**									

Historical Estuarine Residence Times and Performance

Length Characteristics

Rich's (1920) series of fish collections at Point Ellice provide the best data to interpret historical sizes and growth of juvenile Chinook salmon within the Columbia River estuary. Although these results are clearly inadequate to characterize estuary-wide rearing patterns or to quantify absolute abundances, the results demonstrate considerable variation in juvenile size classes as might be expected from the diverse life histories that Rich (1920) identified based on scale analysis.

Rich's (1920) results indicated that small subyearling Chinook salmon continued to arrive at Point Ellice from March until August 1916, while the upper size ranges of subyearlings steadily increased (Figure 69). The earliest collection at Point Ellice in March and April was primarily fry ($n = 102$) that had recently emerged and migrated to the estuary. Subyearlings in the June and July collections were progressively larger, and the average fork length was significantly greater ($P < 0.05$) than the previous month (Table 13). The mean and median fork lengths, however, were essentially identical between the July and August collections ($P > 0.05$, [Table 13]), which may reflect the later influx of smaller fry and fingerlings as well as the continued outmigration of larger smolts to the ocean. The continuous influx of fry and fingerlings of relatively similar size reflects the variability in emergence timing, migration distances, and growth rates among individuals entering the estuary from tributaries throughout the basin.

Estuarine Growth and Residence Times

Rich's (1920) time series of scale samples collected at Point Ellice can be used to estimate the growth of those subyearling Chinook that resided in the estuary for an extended period (e.g., showed evidence of an intermediate scale check [Table 13]). The estimates of estuarine growth of large juveniles collected may be overestimated because of Lee's Phenomenon (Ricker 1992). The minimum and maximum ranges of values, however, represent a mix of size classes.

Of the entire collection, 17% of the subyearlings had evidence of estuarine growth, which accounted for 29–44% of their total length at the time of capture (Figure 71). By July, 70% of the subyearlings exhibited estuarine growth, which contributed 20–66% of their total length (Figure 71). Mean estuarine growth nearly doubled from June to July but remained steady from July to August (Table 14). The proportion of subyearlings with estuarine growth decreased to 58% in August and accounted for one-third to half of the total body length of these fish.

We have no direct measurements of how long individual fish remained in the estuary. To approximate residence times for all subyearlings with an intermediate scale check, we applied literature values for growth rates to total growth in the estuary as estimated from scale analyses (Table 14). Healey (1980, 1991), for example, reported estuarine growth rates from 0.4 to 1.32 mm per day. If we assume an optimistic rate of 1.5 mm per day, then the fish collected at Point Ellice in June that exhibited estuarine growth had remained in the estuary for an average of 18.5

Table 13. Summary table of Chinook subyearlings collected at Point Ellice, May–August 1916. Fork length data from Rich (1920).

Attributes	11 May	12–13 June	19 July	12 and 26 August
Mean (mm)	46.8	76.9	92.3	93.9
Median (mm)	48	78.0	93.0	93.0
Range (mm)	31–85	51–105	56–130	46–125
Subyearling with intermediate check				
Average estuarine growth (mm)	–	27.7	40.0	40.6
Range of estuarine growth (mm)	–	28.7–43.6	19.8–66.4	31.8–52.6
Estimated estuarine residency (days) based on 1.5 mm/day rate	–	18.5	26.7	27.1
Mean FL difference to previous sample (t-test, two-sided P-value)	–	$P < 0.05$	$P < 0.05$	$P = 0.384$
Median FL difference to previous sample (Mann-Whitney W test, two-sided P-value)	–	$P < 0.05$	$P < 0.05$	$P = 0.152$

days with a range of 13.0–25.6 days. The time range increased to 8–57 days by July with an average of 27 days. Residence time values were less variable in August (20–33 days) but still averaged about four weeks.

Assuming a more conservative growth rate of 1 mm per day, estuarine residence times in July and August to the time of capture at Point Ellice averaged approximately 40 days (Table 13). The largest fish at the time of collection typically had the most estuarine growth (Figure 71). These same fish had arrived in the estuary at the smaller size classes (Figure 72). The estimates of growth for the larger fish may be overestimated because of limitations with the scale-interpretation method. Variability within each size class could not be accounted for because Rich (1920) presented the scale analysis as averages by 5 mm size class.

According to the back-calculation results, spring and summer fry migrants (in contrast to fingerling migrants) contributed largely to the estuarine-rearing groups netted in June and July. While fry dominated the early spring collections, it is apparent that at least a portion remained and survived to rear in the estuary.

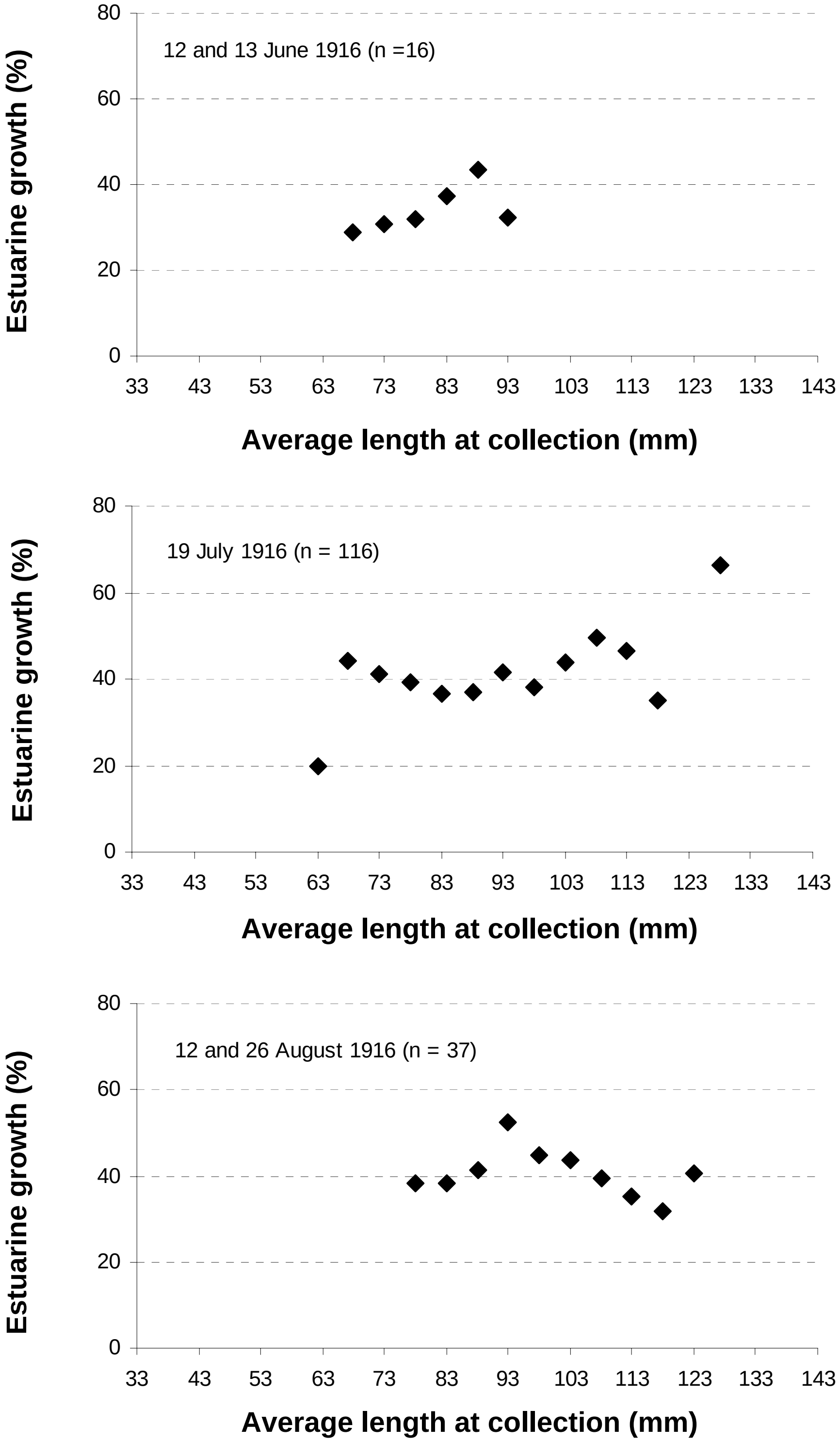

Figure 71. Subyearling Chinook salmon fork length at time of collection and percent of total length attributed to estuarine growth. All fish collected at Point Ellice in 1916 by Rich (1920). Estuarine growth may be overestimated for larger juveniles in the collection.

Table 14. Estuarine and freshwater growth rates from Pacific Northwest river systems. Rates are based on changes in average fork length and monitoring of marked individuals.

Location	Average growth rate	Details	Source
Sacramento River delta (freshwater)	0.86 mm day^{-1}	0.57–1.23 mm day^{-1} in 1980	Kjelson et al. 1982
	0.53 mm day^{-1}	0.40–0.69 mm day^{-1} in 1981	
Sacramento River bay	1.01 mm day^{-1}	1980	Kjelson et al. 1982
Nanaimo River estuary	1.32 mm day^{-1}	(average)	Healey 1980
Fraser River estuary	0.56 mm day^{-1}	1978	Levy and Northcote 1981
	0.39 mm day^{-1}	1979	
Coos Bay	0.29 and 0.54 mm day^{-1}	1987	Fisher and Pearcy 1988
Sixes River	0.9 mm day^{-1}	April–June	Reimers 1973
	0.07 mm day^{-1}	June–August	
	0.5 mm day^{-1}	September–November	
Nitinat estuary (British Columbia)	0.62 mm day^{-1}		Fedorenko et al. 1986

Contemporary Estuarine Residence Times and Performance

Patterns of Abundance

Subyearling Chinook salmon populations in contemporary surveys exhibited a seasonal pattern in abundance but were present in the estuary throughout the year (Bottom et al. 1983, Dawley et al. 1986, McCabe et al. 1986). Peak abundance occurred from May to September, when the majority of the subyearlings migrated into the estuary (McCabe et al. 1986). McCabe et al. partitioned subyearling abundance in the estuary by regions above and below Tongue Point and by pelagic and intertidal habitat within each region. In the pelagic habitat of the upper estuary in 1980, subyearling Chinook showed a bimodal peak in abundance (May and July); while in the pelagic habitat in the lower estuary, subyearling abundance peaked in June. Abundance in the intertidal habitat peaked in June in the upper and lower estuary. In 1981, abundances throughout the estuary peaked in the pelagic habitat in July and in the intertidal habitat in June. The biomodal abundance pattern in the upper pelagic habitat may have been influenced by the eruption of Mount St. Helens in 1980 since that pattern did not occur in 1981.

In the analysis of Jones Beach seine surveys from 1966 to 1972, Dawley et al. (1986) reported bimodal peak abundance timing from May or June and late July or early August. This

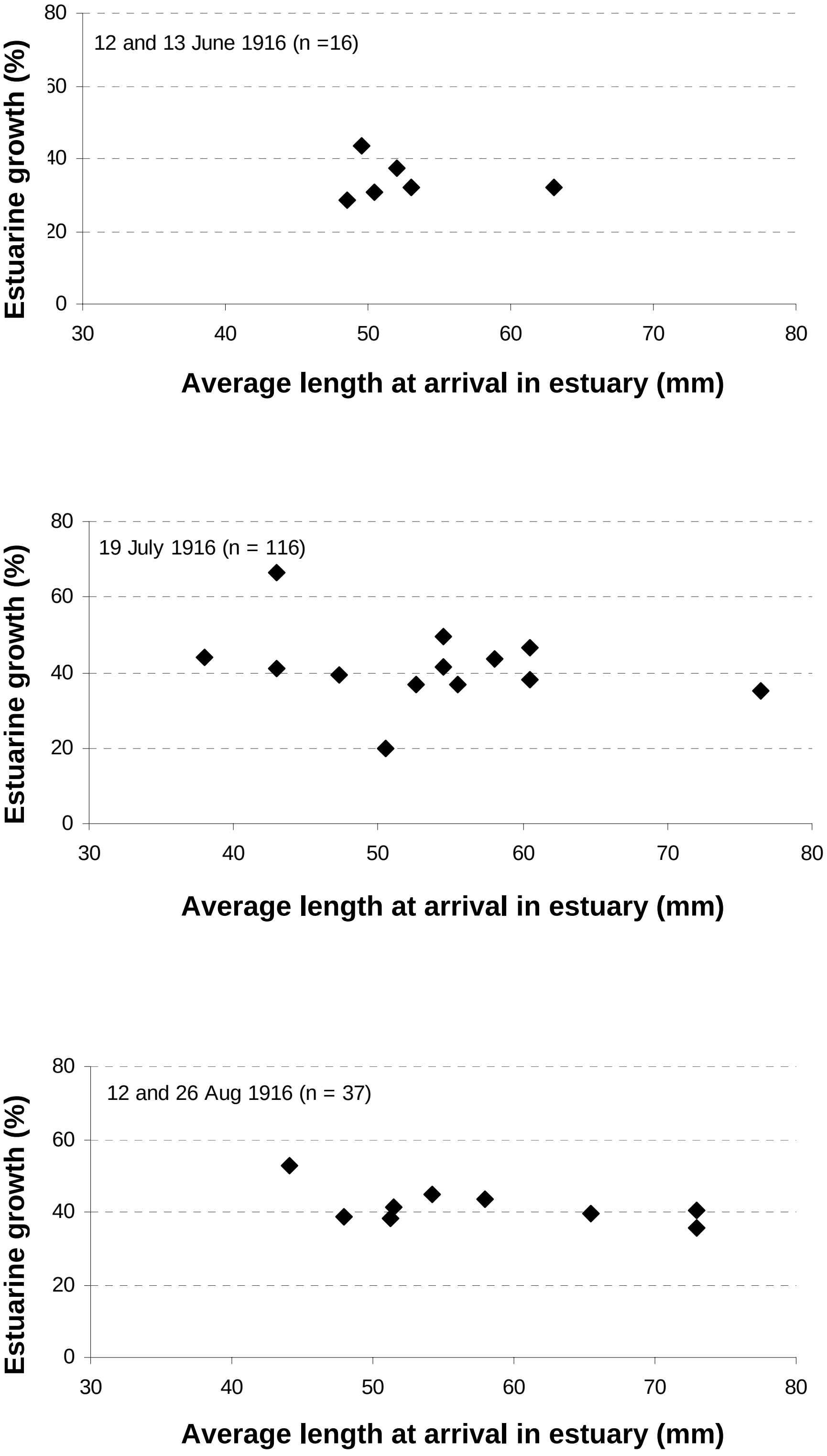

Figure 72. Subyearling Chinook salmon size at arrival in the estuary and percent of total length attributed to estuarine growth. All fish collected at Point Ellice in 1916 by Rich (1920). Average length at arrival to estuary and percent of FL attributed to estuarine growth may be overestimated for larger juveniles in collection.

same pattern, however, was not apparent during the same surveys from 1977 to 1982, when the primary peak in abundance occurred in early May or early June with smaller but significant peaks later in the summer and fall (Dawley et al. 1986). Independent peaks in abundance at Jones Beach for particular populations deviated from the main peaks in the estuary. Abundance of wild subyearling Chinook from the Lewis River, for example, consistently peaked in August at Jones Beach during a study from 1977 to 1979 (McIsaac 1990). Peak catches at Jones Beach were primarily composed of hatchery-reared fish and were highly correlated with the timing of hatchery releases (Figure 73).

McIsaac (1990) determined that peak abundance in the estuary of wild Lewis River juveniles reared in the hatchery were highly influenced by the date of hatchery release and did not necessarily track the timing of naturally reared fish (Figure 74). Hatchery-reared Chinook fingerlings were released between May and September during the three-year study. The arrival times for the first subyearlings at Jones Beach were 3–5 days following the date of release from the hatchery, regardless of the time of year of the release. Conversely, Lewis River wild fish arrived at Jones Beach in early or mid-July during the study except for 1980 migrants, which arrived June 1, probably because of the eruption of Mount St. Helens. The Lewis River study determined that the wild Lewis River juveniles contributed to a higher rate of adult returns than the hatchery-reared stock (McIsaac 1990). Wild subyearlings from the Lewis River have a unique late migratory period to the estuary compared to other lower Columbia River stocks, which may contribute to higher rates of return to the Lewis River (McIsaac 1990).

Habitat Use

The present knowledge of estuarine habitat use in the Columbia River by juvenile Chinook salmon is limited. The only study designed to differentiate habitat use was by CREDDP. However, NMFS biologists primarily surveyed sloping beaches off main channels (demersal slopes), peripheral bays, and open, pelagic habitats (e.g., McCabe et al. 1986). Because NMFS biologists infrequently surveyed small tidal channels, sloughs, or other shallow, off-channel habitats, fish abundance was associated with a limited number of habitat types.

Durkin (1982) reported high concentrations of subyearlings in peripheral bays and shallow intertidal areas, particularly in Cathlamet Bay in 1980. The majority of these subyearlings originated from Washington State hatcheries and may have sought refuge in these shallow areas following their translocation and premature release into the lower estuary after the eruption of Mount St. Helens in 1980 (Durkin 1982). Fish originating from Oregon streams were generally collected in the nearshore habitats on the Oregon side of the river (Durkin 1982). McCabe et al. (1986) extended the analysis of Durkin (1982) and determined that subyearlings were more abundant in intertidal than in pelagic habitats, although such comparisons were difficult, because different gear types were used to sample each habitat type. Stomach analyses showed that the subyearlings were actively feeding in the estuary (Durkin 1982, McCabe et al. 1986). Dawley et al. (1986) and McCabe et al. (1986) found that the mean sizes of subyearlings increased in the deeper habitats and hypothesized that as subyearlings grew, they migrated from neritic to deeper habitats.

Migration routes and habitat preferences of yearling Chinook salmon have been well documented, particularly for hatchery fish. Rich (1920) and Dawley et al. (1986) observed that

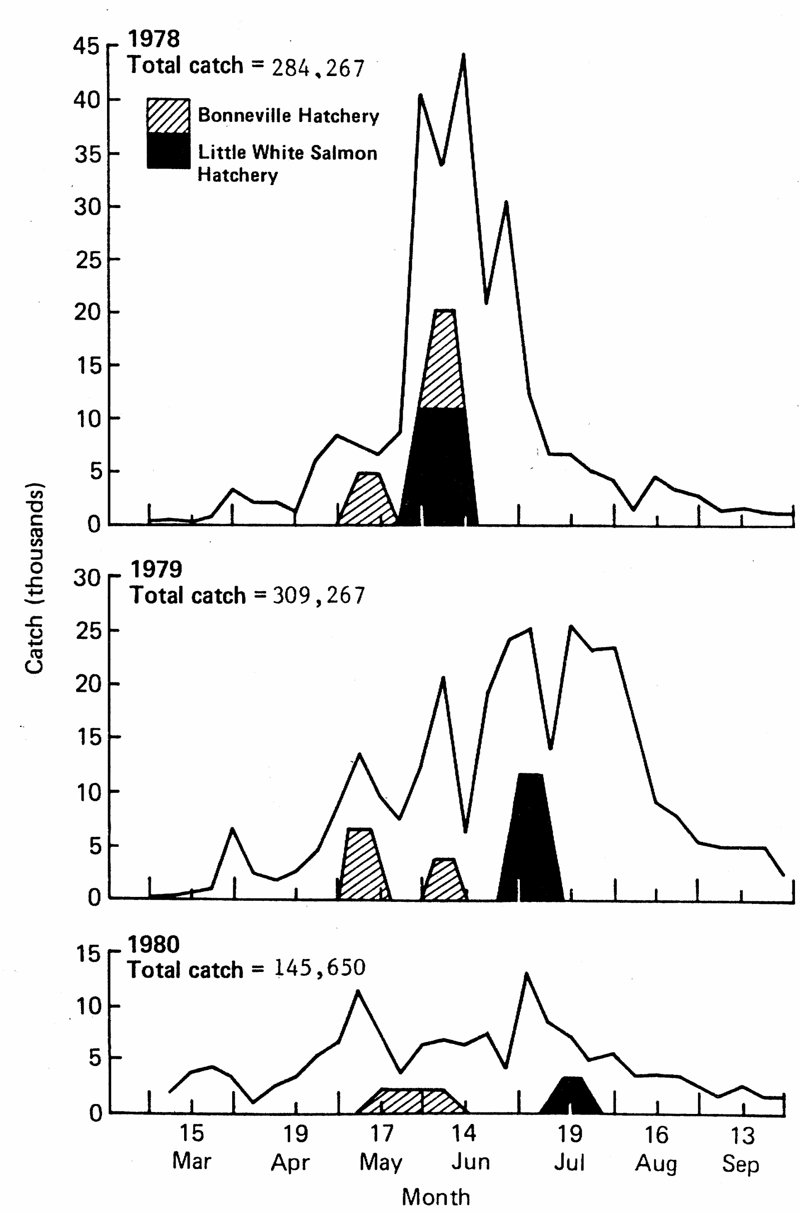

Figure 73. Timing correlation between peak abundance at Jones Beach and the arrival of hatchery-reared subyearling Chinook salmon. The solid black line represents fish of unknown origin (reprinted from Dawley et al. 1986).

yearling migrants (wild and hatchery) found in the estuary before June were concentrated along the shoreline. These migrants comprised the highest catches of yearlings for Dawley et al. (1986). In a three-year study, hatchery-reared yearlings were radio-tagged and tracked through the estuary (Schreck et al. 1995, 1996, and 1997, Schreck and Stahl 1998). These fish primarily used deepwater channels, side channels, and, in two seasons of observation, shallow-water areas (<1.5m deep at high tide) of the estuary.

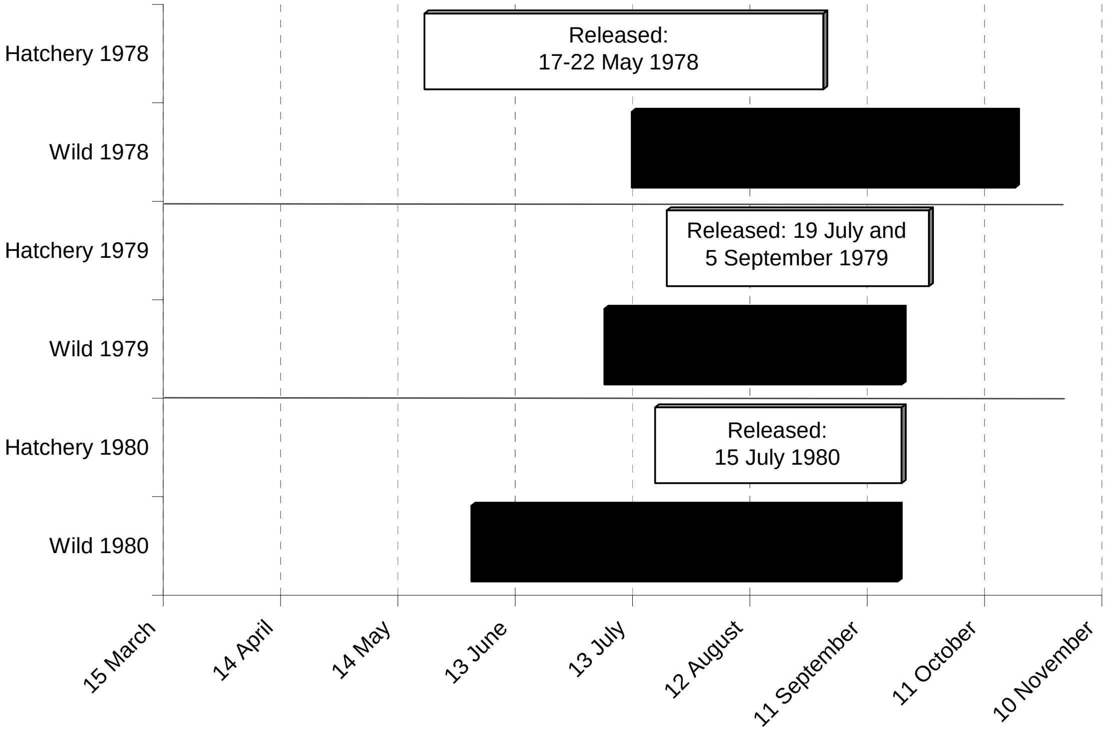

Figure 74. Recovery timing of wild and hatchery subyearling Chinook salmon from the Lewis River at Jones Beach (McIsaac 1990).

Length Characteristics

Recent observations in the fork lengths of juvenile Chinook salmon differed from those described by Rich (1920). Relative to Rich's results, contemporary surveys revealed a narrower range of Chinook salmon sizes and a more homogeneous distribution of size classes (Figure 75). The modern collections lacked smaller subyearlings during early fall (Figure 76). In addition, modern subyearling Chinook salmon collections had a less dramatic increase in length and an earlier stabilization in mean size during the juvenile rearing period compared to the 1916 collections (Figure 69 and Figure 77).

Contemporary size distributions of Chinook salmon during the spring and summer rearing periods differ from those recorded during Rich's (1920) survey. The mean fork length of subyearling Chinook salmon collected by beach seine in May 1916 was 46.8 mm and steadily increased through July (Figure 69). Mean fork length remained the same from July to August (Figure 69). In contrast, subyearling fish of unknown or hatchery origin collected at Megler in 1966 (Figure 76) and McGowan in 1980 (Figure 77), and between RKm 16 and RKm 20 in 1980 (Figure 78) were substantially larger during the initial sampling period (mean FL > 70 mm). Mean fork length did not steadily increase during the spring and summer (Figures 69, 76, and 77), although mean fork length increased by mid-August (Figures 69, 76, 77, and 78).

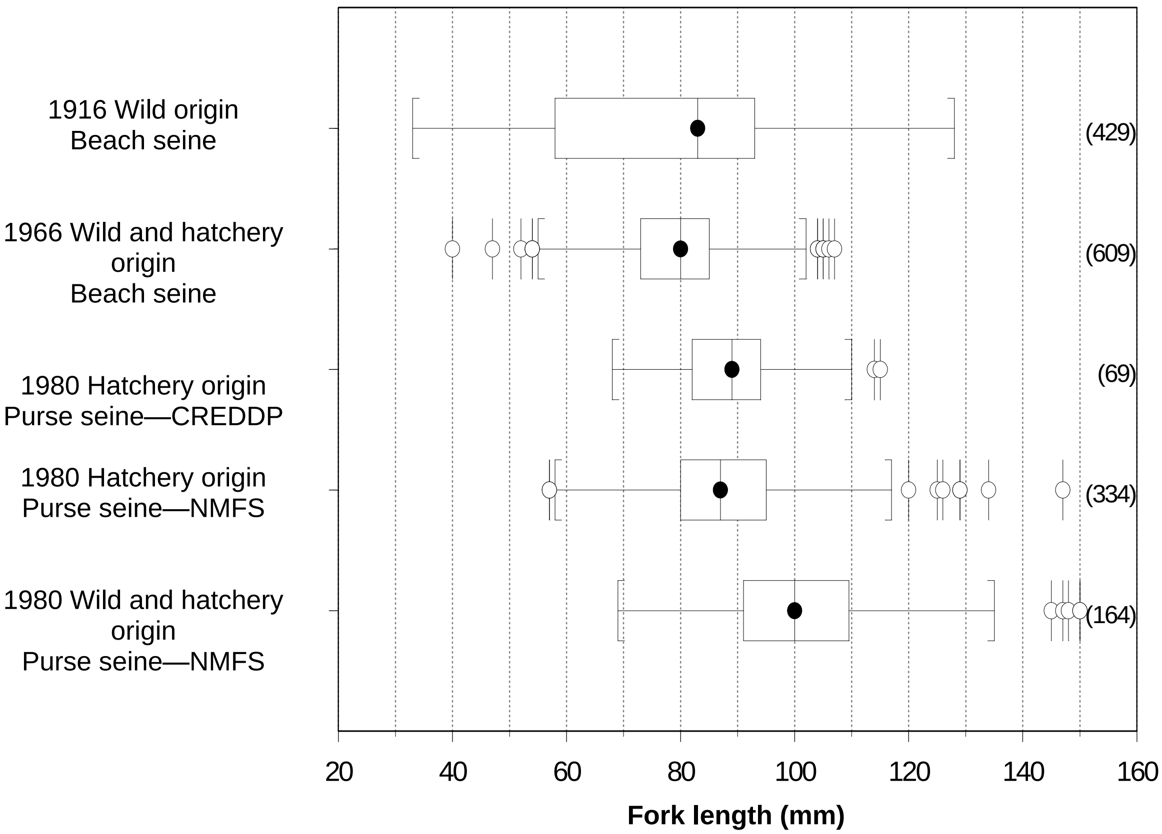

Figure 75. Fork length characteristics of subyearling Chinook salmon collections from three studies in 1916, 1966, and 1980 in the lower Columbia River estuary (Rich 1920, Dawley et al. 1985, Dawley[7]). Data are presented in quartiles with boxes representing 25th and 75th percentiles, whiskers extend to 1.5 multiplied by interquartile range, median is solid circle, all outliers are hollow circles, and number in collection is in parentheses.

Estuarine Residence

Present-day estimates of estuarine residence times are based primarily on mark-recapture studies, because there no contemporary scale data are available to reconstruct life history characteristics and estuarine growth of Chinook salmon. Most of these studies were designed to estimate travel times down to the estuary and survival rates of selected groups of hatchery-reared fish rather than to assess estuarine residency.

The only estimate of estuarine residency was determined from estimated travel rates of marked subyearling Chinook salmon released from hatcheries throughout the basin and recovered at Jones Beach and in the estuary plume. Dawley et al. (1986) established a migration rate of six days or less from Jones Beach to the river mouth as determined by the recovery of fish

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[7] See Footnote 6.

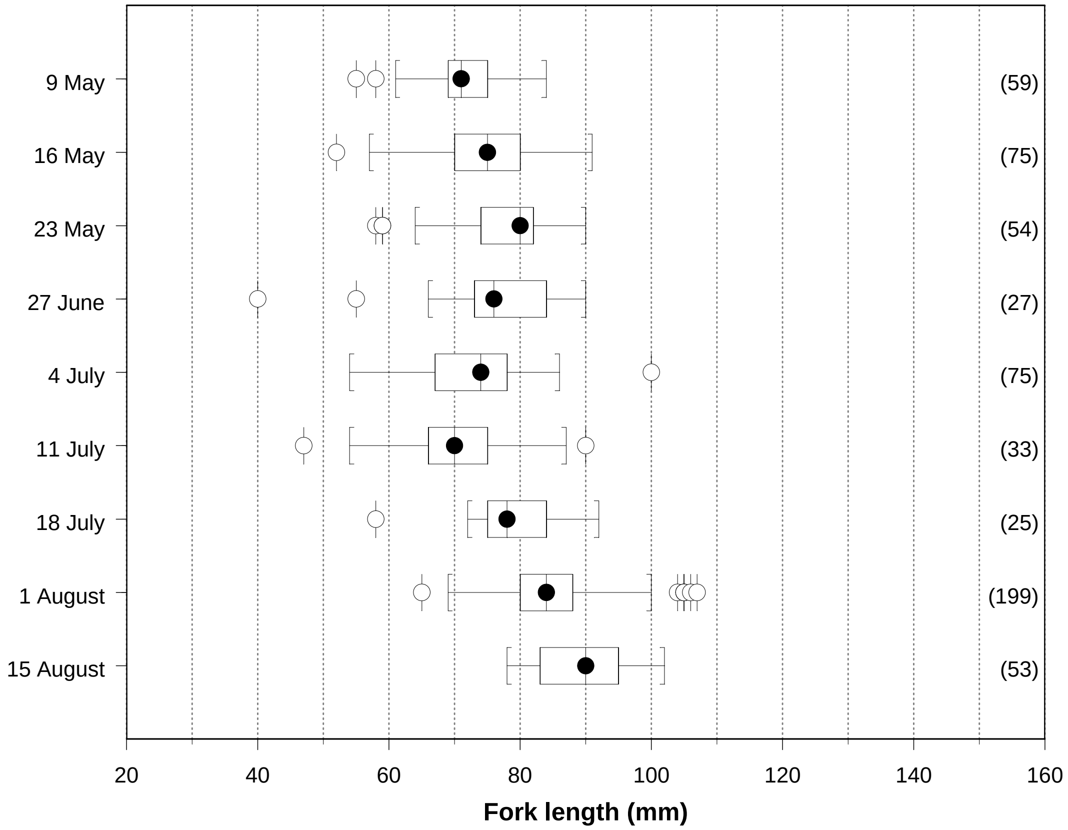

Figure 76. Fork length characteristics of subyearling Chinook salmon of wild and hatchery origin[8] recovered in the Columbia River estuary at Megler, Washington, in 1966. Data are presented in quartiles with boxes representing 25th and 75th percentiles, whiskers extend to 1.5 multiplied by interquartile range, median is solid circle, all outliers are hollow circles, and number in collection is in parentheses.

from 16 uniquely marked groups of hatchery fish. The estimate was based on the date of the first arrival to pass Jones Beach and the date of the first arrival recovered at Clatsop Spit. This rapid movement through the estuary suggests only minimal periods of estuarine rearing below Jones Beach for hatchery-reared subyearling Chinook salmon. This method, however, may not accurately represent estuarine residency, because the timing describes group movement, comprised of hundreds of thousands of similarly marked fish.

There are no representative samples of an estuarine-rearing Chinook population. Dawley et al. (1986), however, recovered six groups of hatchery-reared fry at Jones Beach that had been released in six different locations in the lower Washougal River in Washington on 16–18 June 1969. They determined that these small fry utilized the estuary for an extended period (approximately three months) and moved above and below Jones Beach based on repeat captures of individuals. The average size of these fish was larger than the remaining hatchery-reared fish passing Jones Beach that apparently did not use the estuary (Dawley et al. 1986).

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[8] See Footnote 6.

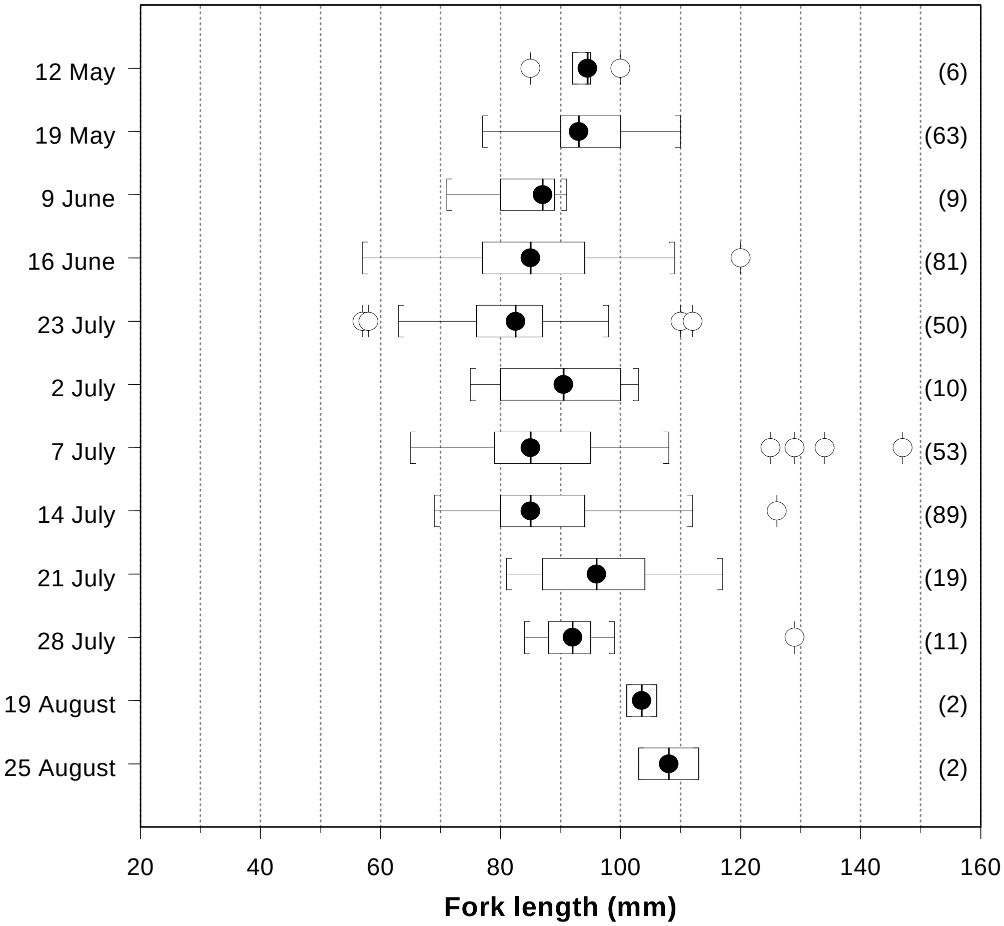

Figure 77. Fork length characteristics of subyearling Chinook salmon of hatchery origin recovered in the Columbia River estuary between RKm 16 and RKm 20 in 1980 by Dawley et al. (1985) and Dawley.[9] Data are presented in quartiles with boxes representing 25th and 75th percentiles, whiskers extend to 1.5 multiplied by interquartile range, median is solid circle, all outliers are hollow circles, and number in collection is in parentheses.

Discussion

Change in Estuarine Life Histories

Chinook salmon in the Columbia River historically exhibited a diversity of life history strategies, using a continuum of streams, rivers, the estuary, and potentially the plume as nursery areas at different times of their life cycle. Anthropogenic changes to the Columbia River ecosystem and the salmon populations have constrained and homogenized the present-day life histories. This interpretation is consistent with recent reconstructions of Chinook salmon life histories upriver (Lichatowich and Mobrand 1995, ISG 2000, Williams in press) and by our comparison of past and present life histories in the estuary. Our assessment further supports the

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[9] See Footnote 6.

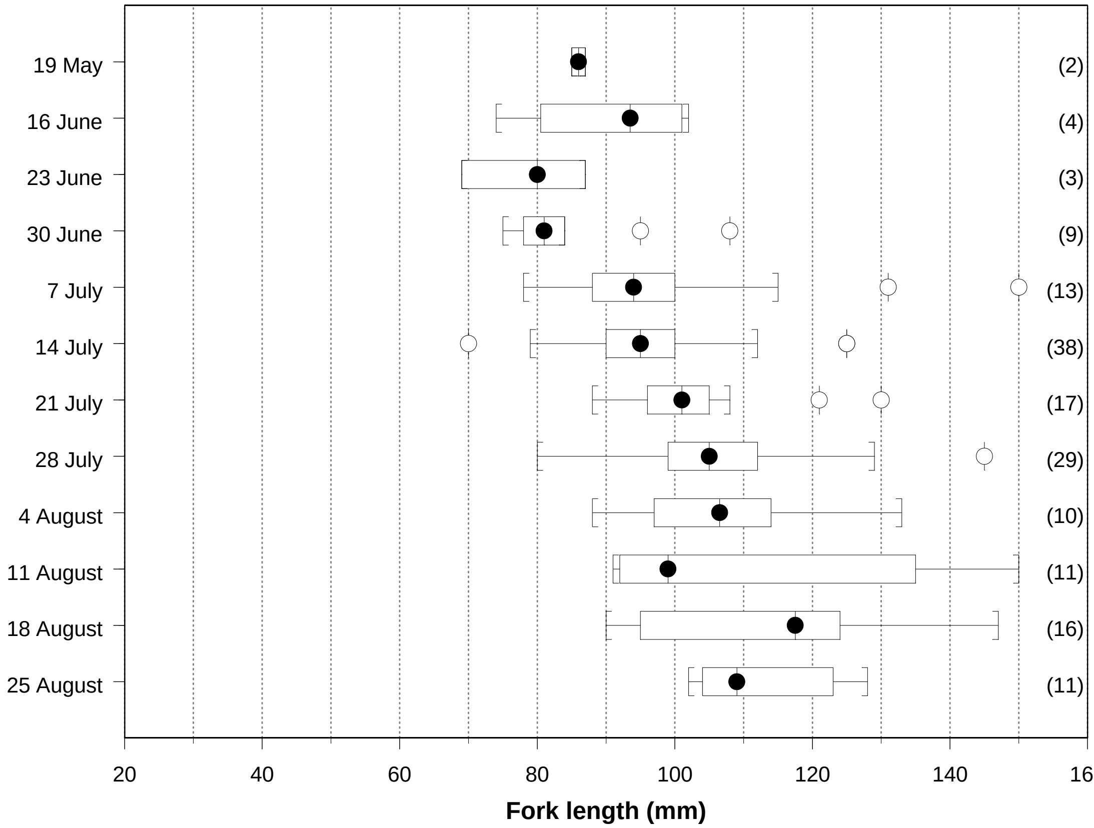

Figure 78. Fork length characteristics of subyearling Chinook salmon of unknown origin recovered in the Columbia River estuary at McGowan (RKm 16) in 1980 by Dawley et al. (1985). Data are presented in quartiles with boxes representing 25th and 75th percentiles, whiskers extend to 1.5 multiplied by interquartile range, median is solid circle, all outliers are hollow circles, and number in collection is in parentheses.

hypothesis that the simple ocean-type and stream-type dichotomy traditionally used to characterize Chinook salmon life histories is an oversimplification of juvenile rearing behaviors.

The diversity of life history strategies of Chinook salmon is evident from the historical collections of Rich (1920). Several forms of ocean-type life histories were described based on fork length, time of collection, and the results of Rich's (1920) scale analyses. Variations in juvenile life histories were apparent by differences in the timing and duration of rearing in natal stream, river, estuary, and ocean environments. Rich (1920) suggested that subyearlings that originated from the same tributary migrated as a group based on similarities in fork length and scale characteristics in each collection. Ocean-type juvenile salmon migrated to the estuary as fry or fingerlings. Fry continuously migrated to the estuary from early spring to August. Fingerlings arrived in the estuary throughout the year. Some remained for extended periods while others probably migrated rapidly seaward.

Our interpretation of Rich's (1920) collections and scale analyses suggest as many as five variants of ocean-type life histories, including fry migrants and four types of fingerling migrants. Subyearlings devoid of scale checks reared in their natal stream and migrated directly to the estuary. Fish with this scale pattern were collected throughout the sampling period. Estuarine rearing subyearlings possessed an intermediate check and, depending on its position, arrived in the estuary as fry or fingerlings. Subyearlings with only a primary check, indicating a riverine life history, did not appear in estuary collections until late fall. Subyearlings with primary and an additional outer check constituted 59% of all fish collected in the fall of 1914 and 1915. Depending on when in the life history the additional outermost checkmark formed, it could be classified as an intermediate check or an annulus (Rich 1920).

Rich (1920) discussed in detail the ambiguity surrounding the interpretation of the annual and intermediate checks. Based on the fork-length ranges and approximate timing at which the outermost check mark may have occurred, we cannot rule out that a component of subyearling Chinook with a riverine and an additional check mark had reared for a time in the estuary.

The uniform sizes of subyearling Chinook salmon in modern collections may reflect the influence of hatchery production on size characteristics or a reduced abundance in diversity of wild fish entering the estuary from upriver or both. This homogeneity of size characteristics is clear when comparing estuary collections from 1916 to 1966 and 1980 (Figure 75). Differences in gear type (purse or beach seine) or year of sampling (1966 and 1980) do not explain apparent changes in juvenile size distribution in the estuary.

While deepwater gear (purse seine and trawl nets) may have been biased for larger fish, we think the size structure of the subyearlings has been truncated and that these changes cannot be explained solely by gear selectivity. Dawley et al. (1986) determined that the purse seine satisfactorily sampled subyearlings as small as 60 mm FL. McCabe et al. (1986) stated that small subyearlings were collected in purse seines and large subyearlings were captured in beach seines early in the summer.

McCabe et al. (1986) found the opposite was true later in the summer when small subyearlings dominated the beach seine collections and large subyearlings were predominately collected in purse seines. These patterns suggest a shift in habitat use among juvenile salmon of various sizes, which may explain some of the differences in salmon size characteristics among gear types and habitats. Such differences do not exclude the possibility that small subyearlings ($\leq$60 mm) may be collected by either gear type.

Hatchery-released fish probably had little influence on the size distribution of Chinook in Rich's (1920) samples. Although it is possible that Rich (1920) collected some hatchery fish, he was confident that all of the subyearlings sampled in the estuary were of wild origin. Hatchery practices in Oregon shifted in 1910 from releasing unfed fry to feeding fry in runway ponds and releasing juveniles as larger fingerlings. In 1916, hatcheries released approximately 95 million fry and fingerlings (Lichatowich et al. 1996). Bonneville Hatchery, the largest production facility at that time, released fingerling Chinook salmon from April to September (Wallis 1964).

The fry that Rich (1920) recovered in March, therefore, were probably wild fish. Rich (1920) contrasted scales of fry collected in the estuary in 31 March and 1–2 April with those from fry sampled at the Clackamas Hatchery in Oregon on 11 April. While all hatchery fry had well-developed scales, many of the wild juveniles did not. Hatchery fry were somewhat larger than wild fry, 36–65 mm FL (n = 62) versus 31–50 mm FL (n = 102), respectively.

The Columbia River estuary may provide critical rearing opportunities and refuge for juveniles prior to ocean migration. Subyearlings in Canadian and the Puget Sound river systems enter the ocean at relatively small sizes (maximum 70 mm FL) and may use the sheltered marine transition areas in the Strait of Georgia and Puget Sound, respectively, as refugia before migrating to the open ocean (Healey 1980, Levy and Northcote 1982, Simenstad et al. 1982, Levings et al. 1986). Because the Columbia River lacks a protected marine embayment, there may be advantages for subyearling Chinook salmon to rear for an extended period and grow to relatively large sizes before leaving the estuary.

Studies in other Oregon rivers suggest that subyearling Chinook salmon may need to migrate at relatively large sizes (100 mm or greater) to have a high probability of surviving in the ocean. Limited data reported for a variety of subyearling Chinook salmon in estuaries reveal maximum lengths in the estuary ranging from 80 mm to about 148 mm (Reimers 1973, Schluchter and Lichatowich 1977, Kjelson et al. 1982, Myers and Horton 1982, Levings et al. 1986, Fisher and Pearcy 1988, Wallace and Collins 1997, MacFarlane and Norton 2002). These results further support the concept that estuaries are important rearing grounds for subyearling migrants, particularly along the open Oregon and California coasts, where no alternative marine transition areas are available to salmon during their seaward migration.

Although larger sizes at migration may often favor ocean survival, the persistence of smaller fry and subyearling life history types among Oregon populations suggests that there is no single threshold size or time that Chinook salmon must migrate to return successfully as adults (Nicholas and Hankin 1988). The wide diversity of historical times and sizes of migration through the Columbia River estuary may have evolved to accommodate a considerable range of oceanographic, estuarine, and riverine conditions. Rich's (1920) scale analyses indicate that juvenile Chinook that reared in the estuary spent at least one week to a few months in the estuary.

Rich and Holmes (1928) examined adult scales and determined that Columbia River juvenile salmon migrated to the ocean as a continuum between ocean-type and stream-type life histories with the whole range of life histories contributing to returning adults. Ocean-type fry and stream-type juveniles were present but minor relative to other (subyearling) life histories. Diversity in residence times, migration times, and size at ocean entry suggests a strategy for maintaining flexibility within and among salmon populations in an unpredictable ocean (Spence 1995) even though larger sizes or later migration periods or both may be advantageous under some environmental conditions (Reimers 1973).

Estuarine residence times inferred from Rich (1920) concur with estimates for the Fraser, Nanaimo, Sixes, and Rogue rivers but differ markedly from more recent estimates in the Columbia River. Many estuarine studies in the region report Chinook rearing in estuaries for several weeks to two months (Healey 1980, Levings et al. 1986, Nicholas and Hankin 1988, Reimers 1973). In contrast, contemporary estimates of residency for subyearlings in the Columbia River estuary were about a week for 16 groups of marked hatchery fish migrating past Jones Beach and recovered in the lower estuary (below 18 RKm [Dawley et al. 1986]), except for Washougal River hatchery juveniles that reared for approximately three months in the estuary after being released early at a very small size.

Because individual fish were not monitored and only a small number of fish from each marked group were recaptured in the lower estuary, we cannot be certain whether the estimated residence times are characteristic of most contemporary populations. Residence times were derived from the first fish from each tagged group captured at Jones Beach and at the estuary mouth and, therefore, do not characterize the range of estuarine residence times. Dawley et al. (1986) concluded that the majority of fall Chinook salmon fingerlings remain in the estuary for a relatively short period. If this is correct, then the residency of most ocean-type Chinook salmon has declined relative to the historical estimates reported by Rich (1920).

Our interpretations of past and present juvenile life histories for Chinook salmon are clearly limited by the lack of basic biological surveys in the Columbia River estuary. The range of life history types, estuarine-residence times, and growth estimates are based upon a comparison of three years of data (1916, 1966, and 1980) at a single site in the lower estuary. These data are not sufficiently comprehensive to depict the former or present diversity of salmon found among the full variety of habitats throughout the estuary or to describe variability in rearing behaviors over a time period. Without independent surveys or methods to validate Rich's (1920) results, scale analyses from 1914 to 1916 could be subject to unknown errors or misinterpretations. The inability to distinguish an annulus from an intermediate check prevents precise classification of some life history types. But the effect of most past or present data limitations would seem to underestimate rather than overestimate the diversity of rearing behaviors in the basin.

The lack of research on subyearlings in shallow estuarine habitats, particularly tidal channels, sloughs, and marshes, also may limit understanding of life history diversity as well as the rearing requirements of Columbia River Chinook salmon. These shallow habitats, which are heavily used by subyearling salmon in other Northwest estuaries, may be particularly important off-channel refugia in a high energy, river-dominated system such as the Columbia (Healey 1982, Levy and Northcote 1982). While limited sampling has occurred in the lower Columbia River estuary (below 75 RKm), the upper estuary (above 75 RKm) has not been studied. A variety of sloughs and side channels in the upper estuary offers potential refugia and rearing habitat for downstream migrants.

Modern methodologies used to monitor groups of salmon as they pass through the Columbia River estuary do not differentiate among various life history types. Because of the difficulty of estuarine recovery of marked salmon, residency estimates have been based on a very small proportion (<6%) of the marked population (Dawley et al. 1986). Such estimates are derived primarily from hatchery-reared fish, which constitute more than 95% of the marked population and are biased toward larger fish that can retain tags (Dawley et al. 1986). Contemporary estuarine peaks in salmon abundance have been associated with the timing of hatchery releases (Dawley et al. 1986). Hatchery influence on patterns of salmon abundance may help to explain the relative uniformity of juvenile size classes because of the release of large groups of similarly sized subyearling or yearling Chinook. Reported size distributions, however, may underestimate present-day diversity in the estuary because of the limited sampling and recovery design, which targets groups of marked hatchery fish and ignores smaller subyearlings and the shallow-water habitats they may prefer.

While basic data on the life history of wild Chinook salmon was available in the early 1900s, the lack of scale collections and pertinent data in recent years prevents us from similarly classifying the juvenile life histories of contemporary salmon populations. We have found a limited scale archive for estuary samples of coho and yearling Chinook salmon only, and these have yet to be interpreted. Interpretation of the coho salmon scales may be particularly useful given the multiple life histories of juvenile coho salmon described in the South Slough National Estuarine Research Reserve in Oregon and in several other coastal estuaries (McMahon and Holtby 1992, Miller and Simenstad 1997, Miller and Sadro 2003).

The diversity of Chinook salmon life histories we described from historical Columbia River data is consistent with the variety of life histories reported in other Northwest estuaries. The Rogue and Sixes rivers estuaries, two small systems on the southern Oregon coast, had a similar or greater number of early life history types than those documented in the Columbia River (Schlucter and Lichatowich 1976, Reimers 1973). Healey (1980) and Carl and Healey (1984) described at least three genetically distinct life history types in addition to various times of migration for Chinook salmon in the Nanaimo River basin on Vancouver Island, British Columbia.

In the “Conceptual Framework for Evaluating Habitat Conditions” section (page 21), three generalized life history strategies (Figure 11) were proposed for Chinook salmon in the Columbia River basin. These strategies were distinguished by length of time spent in each freshwater environment, time spent in the estuary, and time and size at ocean entrance. From the analysis of Rich’s (1920) data, this simple model was expanded to recognize six life history types in the Columbia River, including five variants of subyearling life history (Figure 79).

Based on Rich’s results and the extent of freshwater habitat available before most Columbia River dams were constructed, we hypothesize that one or more Chinook life history types historically used natal streams, mainstem rivers, or estuarine environments as alternative nursery habitats, with each brood of Columbia River salmon represented by a continuum of rearing and migrant behaviors spanning an 18-month period (Figure 79). By contrast, we infer that ocean-type Chinook salmon with estuarine rearing life histories are now substantially reduced in importance, leaving three principal life history types in the basin:

1) fry migrants,
2) subyearling migrants that rear in natal streams (including hatchery-reared juveniles), or main rivers or both, and
3) yearling migrants (Figure 79).

Historical and Contemporary Factors Affecting Salmonid Life Histories

The watershed, estuary, and salmon populations have undergone significant changes in the 85 years since Rich’s (1920) study. Many changes, however, already had occurred prior to 1916:

- commercial harvest of salmon reduced spring and summer Chinook runs to remnant levels,

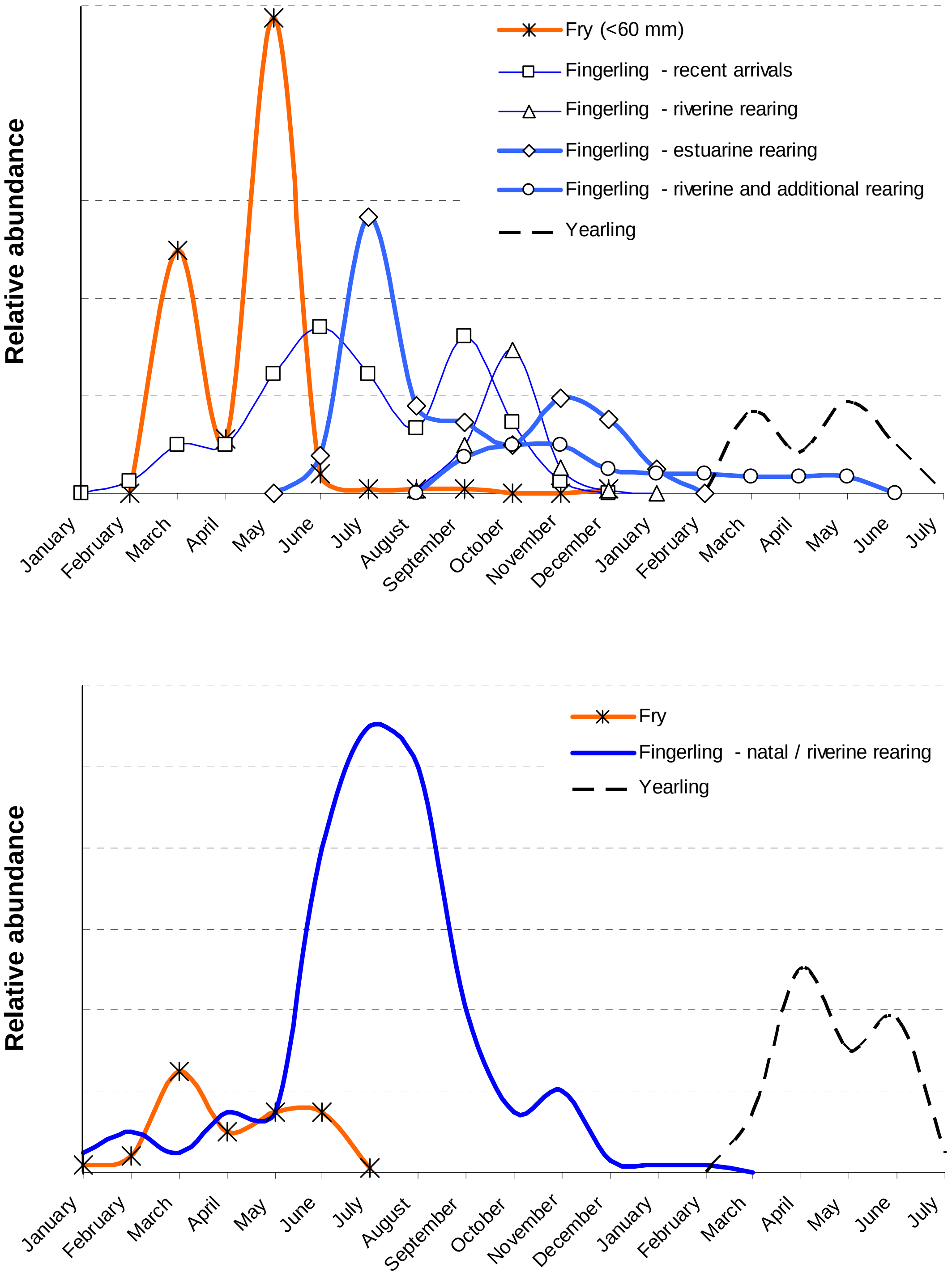

Figure 79. Historical and contemporary early life history types for one broodyear of Chinook salmon in the Columbia River estuary. Historical timing and relative abundance (top) based on historical sampling throughout the lower estuary (Rich 1920). Contemporary timing and relative abundance (bottom) derived from Dawley et al. (1985) sampling at Jones Beach. Data were smoothed for appearance.

- migrant juveniles suffered massive losses to irrigation diversions, timber harvest, and related activities such as roads and splash dams that impacted watersheds and stream channels,
- large-scale mining was active in many watersheds, and
- sheep and cattle grazing were extensive (Lichatowich and Mobrand 1995, Lichatowich et al. 1996).

The results interpreted from Rich's (1920) study, therefore, may not accurately reflect the full diversity of life histories that existed prior to European settlement in the region.

The apparent increased proportions of larger subyearlings with short estuarine residence times is consistent with the life history response we might expect from the changes that have affected the Columbia Basin and salmon populations since Rich's survey. As suggested by our conceptual model (Figure 9) and supported by our assessment of estuarine changes in the previous four sections, factors reducing diversity of estuarine rearing behaviors may include:

- the quantity and quality of salmon habitat, both in the estuary and upriver,
- reduced genetic diversity through harvest pressures, population extinctions, and other causes, and
- the effects of hatchery rearing, release, and fish transportation practices on salmon size distributions and phenotypic behaviors.

Although we cannot distinguish their individual contributions to life history change or salmon decline, the historical factors discussed in the following subsections together may largely determine the present-day performance of Chinook salmon in the estuary.

Salmon harvest

Effects of commercial harvest on particular components of the total Columbia River production of Chinook salmon were realized well before the start of the 20th century. Commercial harvest of adult salmon runs began in the early 1800s (Figure 80), when salmon were so abundant that it was hard to imagine that there would not be enough for everyone (Hume 1893). Commercial fishermen initially targeted spring-run Chinook adults, the superior canning variety (Lichatowich et al. 1996). Harvest pressure intensified in the 1860s.

As the number of the spring-run adults diminished, commercial fishermen shifted to fall-run Chinook in 1890. Concurrently a significant reduction in the number of adults returning to spawn became apparent in 1890 in the Snake River basin (Evermann 1895). A one-month delay in the spawning time of mainstem Snake River fall-run adults also was observed consistently for several years (Evermann 1895). Evermann noted that the adult runs passing over Lower Salmon Falls Dam on the Snake River, which usually arrived in late July and early August, did not arrive until early September. Adult runs in the Payette and Salmon rivers in Idaho completed the upriver migration at least one month earlier than the Snake River run and in

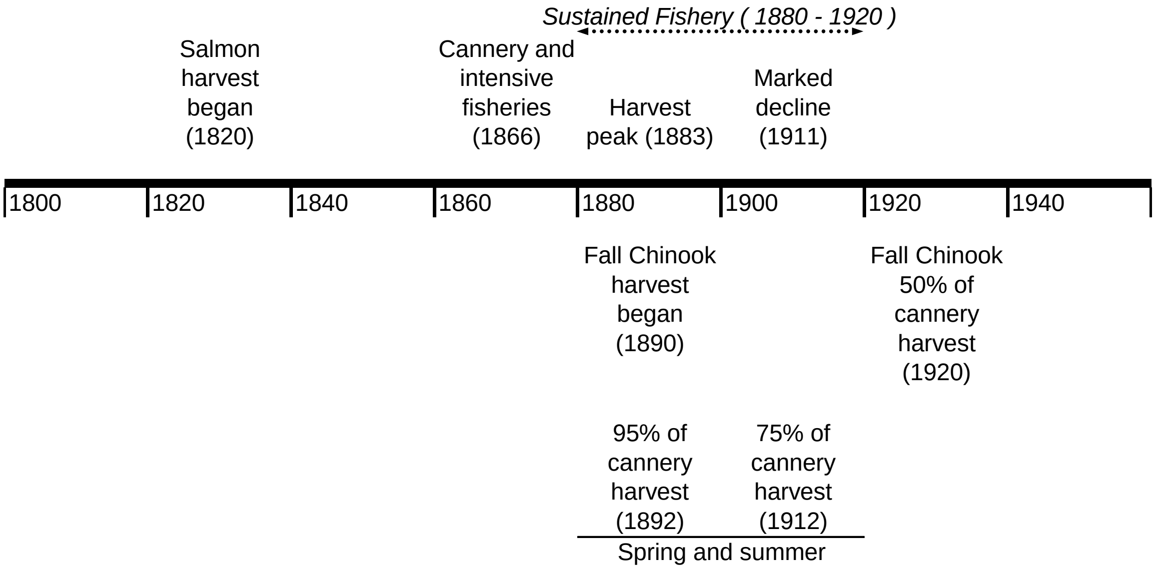

Figure 80. Harvest timeline for Chinook salmon, 1800–1916 based on significant events presented by Oregon State Board of Fish Commissioners (OSBFC 1890 and 1892), Hume (1893), Craig and Hacker (1940), Fulton (1970), Beiningen (1976), Smith and Wahle (1981), and Lichatowich and Mobrand (1995).

slightly higher numbers compared to other years. Fishing pressure was potentially affecting specific components of the Chinook salmon run in addition to the natural variability associated with populations.

The temporal and spatial differentiation of the adult runs increased the vulnerability of each subbasin population to fishing pressure, which has further compounded their natural volatility. Rich and Holmes (1928) commented repeatedly that fishery managers must regulate harvest of the entire adult run and not target discrete segments to minimize the impact on any single population. The shift in harvest from spring- to fall-run stocks in the late 1800s could have redirected the fisheries impact onto the mainstem Snake River adult run while allowing the Payette and Salmon rivers adult runs to recover. By 1938, Rich (1943) reiterated his support of ecosystem-based harvest regulations after completing fish counts and noting the greater abundance of fall-run adults, which had recently received protection by the closure of the lower river fall-run fishery starting on 25 August 1938. The effects of the harvest pressure were obvious from the fish counts going over Bonneville Dam, since harvest was shifted back to spring-run Chinook salmon, and their abundance fell accordingly.

One effect of harvest and other intensive selection pressures in the Columbia Basin may have been the development of a lesser number of relatively discrete salmon runs. Chinook salmon in the Columbia historically may have been composed of a broad continuum of spawning populations distributed across the entire habitat spectrum (Miller and Brannon 1981, Beaty 1992). Multiple changes during the past century, including the effects of intensive fisheries, may have selectively eliminated components of this continuum while promoting others.

Thompson (1951) suggested that the upriver bright stock, a distinct group of fall Chinook salmon that spawns in late August to September, may have developed from the late tail of the summer run, which was protected by a long-term fishery closure. Rapid growth of Columbia River brights may have been aided by additional habitat opportunities created by heavy exploitation on other stocks (Beaty 1992). Today a majority of the fall Chinook salmon run still passes Bonneville Dam during late summer (Figure 81).

Because the early life history strategies of Chinook salmon are directly linked to the seasonal timing of the adult runs, changes in spawning populations during the past 80 years may have directly affected patterns of estuarine rearing. Rich (1925) analyzed scales from returning adults in the Columbia River and determined that the majority of the spring-run adults had stream-type life histories and the fall-run adults were dominated by ocean-type life histories. However, both types were present from May to September (Figure 82). Summer-run adults exhibited both life history types depending upon where in the basin the juveniles originated. Snake River basin summer-run adults typically are stream-type migrants, while mid-Columbia River summer-run adults (i.e., Hanford Reach spawners) are ocean-type juveniles.

Fisheries that inadvertently targeted specific populations of returning adults reduced the production of the juvenile life histories associated with those populations. By decreasing the abundance of wild populations and replacing a broad continuum of spawning populations with a few discrete stocks, harvest and other selective pressures have diminished life history diversity in the Columbia River basin, including some subyearling life history types that may have used the estuary.

Habitat loss

Habitat degradation and its adverse effects on salmon were noted as early as 1894, when mining in the Snake River watershed destroyed Chinook salmon spawning beds and contributed to the collapse of a popular American Indian fishing site (Evermann 1895). Habitat loss and degradation has been and continues to be a major influence on the abundance and diversity of salmon in the Columbia River (Nehlsen 1995, Lichatowich et al. 1996, Lichatowich 1999). Chinook salmon populations from the upper Columbia River basin in British Columbia and Alberta, Canada; middle Snake River basin and above, and the greater part of the Deschutes River basin in Oregon have been extinct for at least 40 years because of impassable dams (Figure 2). The blocking of upstream passage reduced basin-wide productivity and diversity of salmon.

In the Snake River, ocean-type Chinook salmon now occupy only 17% of the historical habitat (Hassemer et al. 1997). The Deschutes River basin, now inaccessible above 161 RKm, encompassed a highly connected cold-water tributary system (Metolius River), an extremely large warm-water tributary system (Crooked River), and a mainstem system. It may have been one of the greatest contributors to Chinook salmon production in the Columbia River and probably included a wide variety of life history types associated with the diverse freshwater habitats (Burke et al. in prep.).

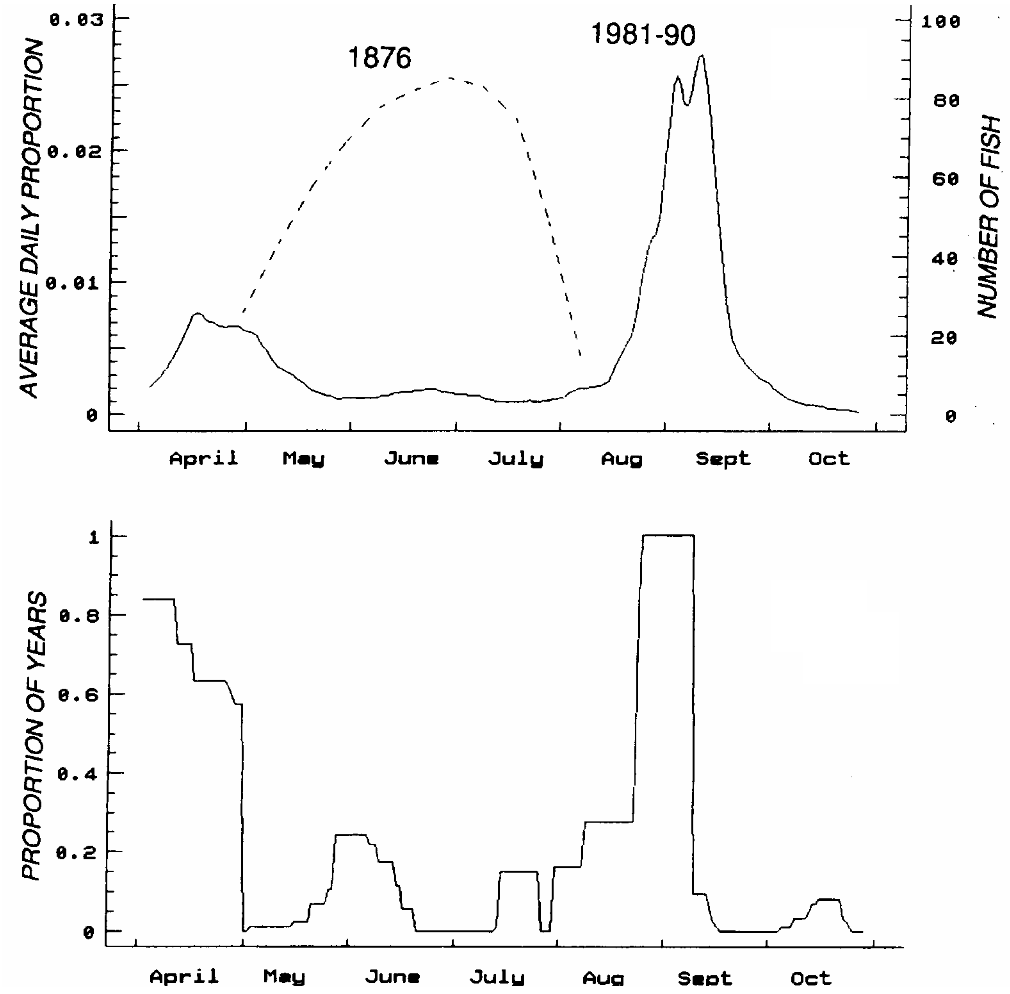

Figure 81. The effect of seasonal protection of salmon runs in the Columbia River. Adult run timing (top) reconstructed from historical gill-net records for 1876 and adult escapement at Bonneville Dam, 1981–1990. Seasonal protection (bottom) of salmon runs, 1877–1963 (reprinted with permission from Beaty 1992).

Loss and degradation of habitat throughout the Columbia River basin has reduced its productive potential and concentrated the remaining salmon into more limited and highly fragmented regions. Dam construction, together with temperature increases in the main stem and in lower subbasins, have diminished habitat opportunity upriver and substantially reduced the proportion of ocean-type migrants that are now produced in the Columbia (ISG 2000, Williams in press).

Loss of subyearling migrant types from summer and spring spawners probably has occurred in many upriver areas that historically offered optimal growth opportunity, particularly in the warmer middle portions of Columbia subbasins (Lichatowich and Mobrand 1995, ISG 2000, Williams in press). Because subyearling migrants typically reside in the estuary for longer periods and use different habitats than those with yearling life histories, such losses could have

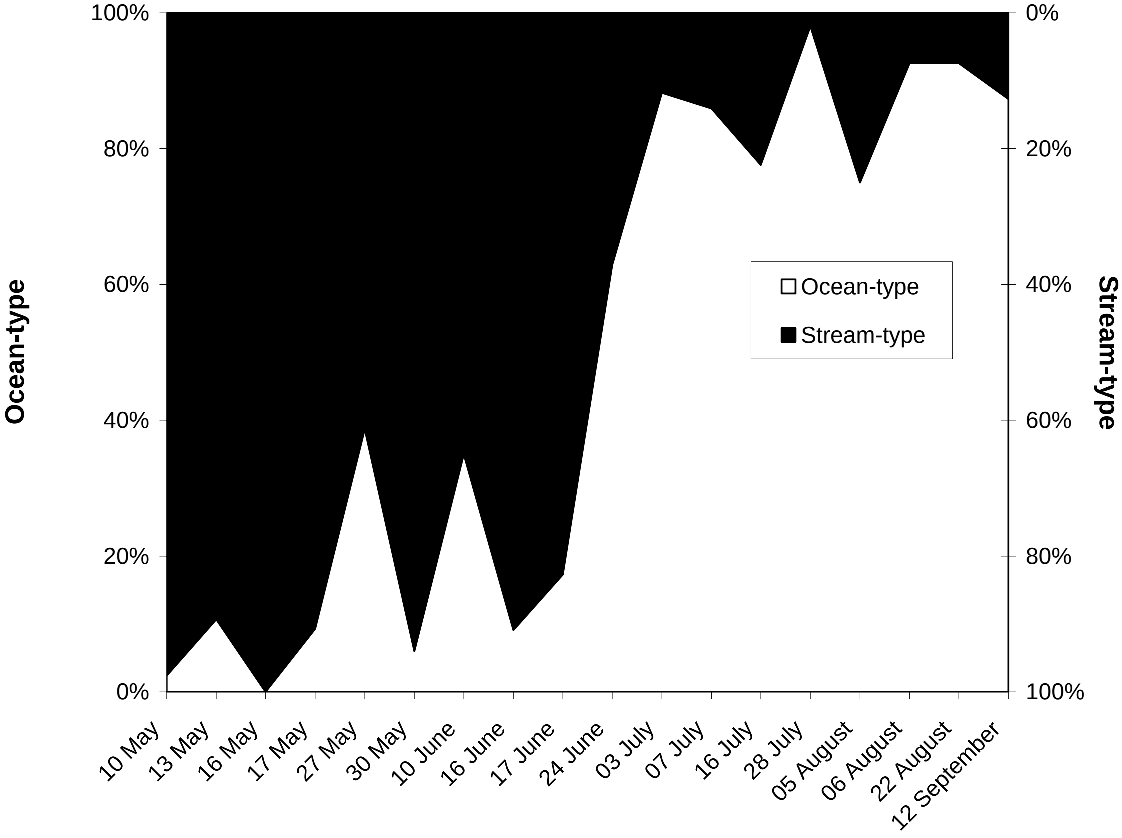

Figure 82. Interpretation of early life history behavior based on scale patterns from returning salmon adults collected in the Columbia River estuary, 10 May–12 September 1919 (Rich 1925). Sample dates are not equal time intervals.

an important influence on contemporary patterns of estuarine rearing by Chinook salmon and could leave vacant various shallow-water estuarine habitats favored by smaller ocean-type juveniles.

Habitat changes within the estuary (see the "Estuarine Habitat Opportunity" section, page 89, and the "Estuarine Habitat Capacity" section, page 127), however, also could account for the loss of some subyearling life history types. Tidal marshes and swamps within the Columbia River estuary have been reduced by 65% (Thomas 1983). Use of these habitats by salmonids currently is being studied in the Columbia River estuary and results are not yet available, but tidal marshes and swamps are productive rearing areas for small Chinook and chum fry in other Northwest estuaries (Healey 1982, Levy and Northcote 1982). Additional wetland losses have not been quantified in the tidal freshwater region between 75 RKm and 235 RKm (Bonneville Dam). Losses of tidal riparian and floodplain habitats in this region from diking, filling, and railroad construction also appear to be significant. Other types of shallow habitat may have increased in the estuary (see the "Estuarine Habitat Opportunity" section, page 89), including an estimated 7% in the amount of shallows and flats, primarily because of the artificial creation of islands from disposal of dredged material (see the "Estuarine Habitat Capacity" section, page 127).

Yet these habitats do not provide the same functions as the marginal wetlands that have been removed, nor do they mitigate for the estimated 15% reduction in the estuary's historical tidal prism (Sherwood et al. 1990). Regardless of other shallow-habitat gains, considerable diking of wetland and floodplain habitats may have reduced the capacity of the estuary to support ocean-type subyearling salmon and may contribute to the apparent underrepresentation of these life histories in recent studies relative to the period of Rich's (1920) survey.

Irrigation

Cropland irrigation in the Columbia River basin withdraws more water than industrial, hydropower, and municipal sources with devastating effects on juvenile and adult salmonids (Lichatowich and Mobrand 1995, NRC 1996, Lichatowich et al. 1996). The construction of ditches and irrigation dams in Columbia River stream systems began in the mid-1800s, accelerated in the early 1900s, and continues today successfully converting arid lands to cultivated fields. In the early 1900s irrigation ditches diverted 90–97% of the Yakima River from April to late October, carrying juvenile salmonids into ditches and blocking the upstream migration of adults (Pacific Fisherman 1920). High rates of mortality occurred when juveniles were dispersed onto cultivated fields and became trapped when irrigation ceased and ditches dewatered (Pacific Fisherman 1920). A single watering event in a Yakima River valley sacrificed an estimated 4.5 million migrating juveniles (Pacific Fisherman 1920).

Irrigation practices also have effectively blocked juvenile and adult salmon migrations. Temporary push-up dams and irrigation diversions left downstream channels with little or no water, hindering juvenile and adult passage and reducing water quality (NRC 1996, PFMC 1999). Low flows from irrigation withdrawals also produced extreme water temperatures, rendering some streams lethal and impassable to salmonids (Lichatowich and Mobrand 1995, Lichatowich et al. 1996). We can only surmise the potential losses from diversions and dams since no quantified assessments are available (NRC 1996). Thermal barriers to the lower reaches of many Columbia River tributaries, however, may have effectively blocked the downstream migrations of ocean-type juveniles (ISG 2000, Williams in press). Thousands of unscreened diversions still remain in the basin today.

Flow regime

Diking and flow regulation have drastically altered the available habitat and flow regime encountered by salmon in the Columbia River and the estuary (see the "Changes in Hydrological Conditions" section, page 47, [Figure 28]). Diking of islands and margins of the estuary has eliminated refugia from high flows once available to juvenile salmon. At the same time, flow regulation has reduced spring-freshet levels and dams have created impoundments that alter the migratory habitat for juveniles traveling downstream. Prior to flow regulation, flow levels were greater and the variability within short time periods was higher (Sherwood et al. 1990).

Floodwaters of the Columbia River historically inundated the margins and floodplains along the estuary, permitting juvenile salmon access to a wide expanse of low velocity marshland and tidal channel habitats. The greater seasonal variability of estuarine velocities and depths prior to flow regulation also may have allowed a greater diversity of estuarine rearing behaviors by juvenile salmon. Reduced habitat potential coupled with an altered flow regime probably has reduced the productive capacity of the estuary for juvenile salmon.

The salmon data analyzed in this study encompass periods of a relatively free flowing river in 1916, a highly regulated river in the early 1970s, and the added effects of a volcanic eruption in 1980. Long-term river flow values are available at The Dalles gauge from 1878 to the present (USGS 2001). The relevant flow years are presented in Figure 83, including estimates for the Willamette River (see the "Changes in Hydrological Conditions" section, page 47). The May 1980 eruption of Mount St. Helens, which added a huge quantity of silt and logs to the lower Columbia River estuary, hampered collection efforts until June (Dawley et al. 1986).

Excluding the Mount St. Helens eruption, the sampling seasons of 1966 and 1980 were relatively benign, while the 1916 sampling season had one of the latest spring freshets on record, with flows on July 5 exceeding 20,000 m^3s^{-1} (Figure 83). Although Rich (1920) made no mention of the river conditions, flows would have been between 10,000 m^3s^{-1} and 23,000 m^3s^{-1} during Rich's sampling (Figure 81). Flows in 1966 and 1980, however, probably were close to 5,000 m^3s^{-1} and 10,000 m^3s^{-1}, including the Willamette River's contribution.

The importance of shallow-water habitat as refugia for salmon fry is epitomized by the collection of juveniles less than 60 mm in the estuary during and after the peak freshet in 1916 (Rich 1920). The mid-July sample of 1916 included subyearlings that had resided in the estuary for at least 8–57 days, which encompassed the peak flow period. Prior to major physical alterations, the marginal areas of the estuary would have extended outward, expanding the surface area of the estuary dramatically and increasing the area of shallow, low velocity habitat accessible to smaller juvenile salmon. To maintain their position within the estuary during 1916 peak flows, the smaller subyearlings must have sought refuge in shallow peripheral marshes and other off-channel habitats that would have been flooded.

Artificial propagation of salmon

The capacity of the estuary to support juvenile salmon may be influenced by the timing of hatchery releases and the abundance of hatchery juveniles in the Columbia River estuary. Several studies suggest that wild Chinook salmon may have a much broader migration period to the estuary than that of hatchery fish.

Reimers and Loeffel (1967) beach seined seven tributaries in the lower Columbia River subbasin until subyearlings were no longer captured. Their results showed considerable variability in the duration and completion of outmigration from each tributary into the estuary (Figure 82). The Klaskanine River population, for example, concluded their outmigration within one month and ended by the middle of June. The North Fork Lewis River population entered the estuary over a four-month period and did not complete their seaward migration until the middle of October (Figure 84). These results are consistent with McIsaac's (1990) study of the North Fork Lewis River 1977–1979 brood, which similarly documented considerable variability in wild fish migration timing to Jones Beach between sample years (Figure 75). The prolonged period of fry emergence and variable timing of seaward migration in the North Fork Lewis River population indicates a variety of life histories among wild fish.

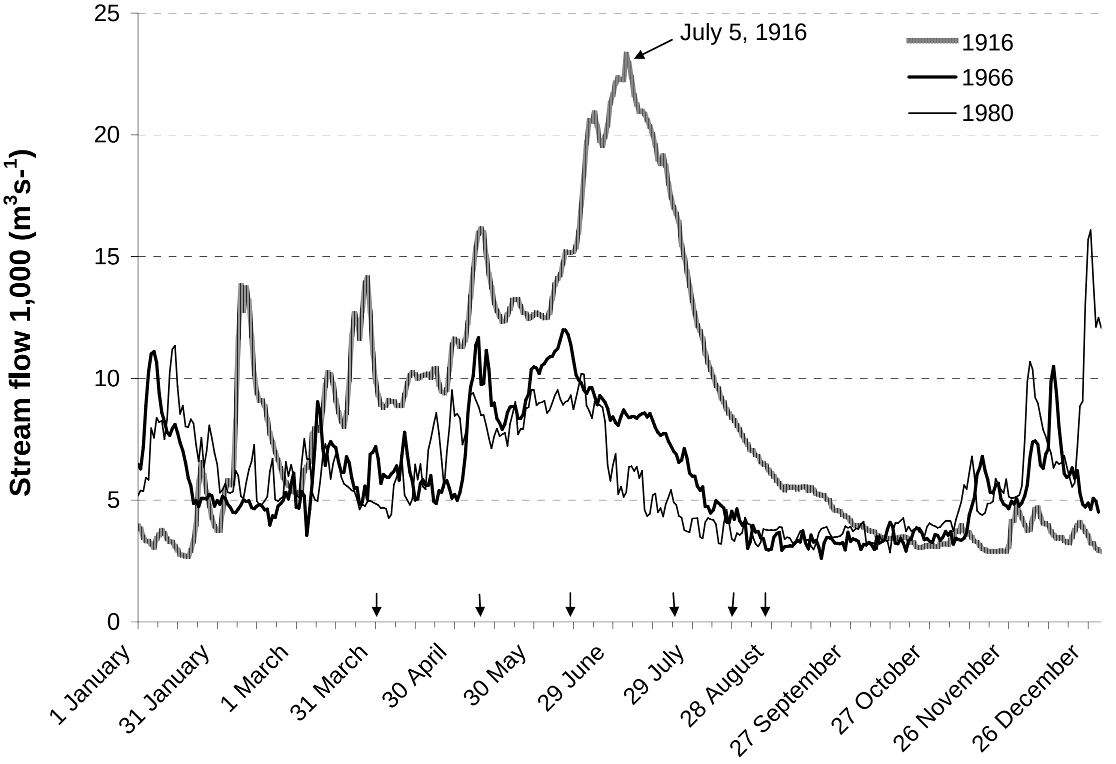

Figure 83. River flows (cubic meters per second) for 1916, 1966, and 1980. Arrows at base of graph represent sampling dates in the lower estuary by Rich (1920). Flows compiled from The Dalles gauge (USGS 2001) and estimates of Willamette River contribution at Salem, Oregon (see the "Changes in Hydrological Conditions" section, page 47).

Several studies have found that hatchery-reared Chinook salmon migrate within a relatively narrow period. Dawley et al. (1986) correlated the estuarine abundance and time of entry of subyearling Chinook sampled at Jones Beach with their time of release from the hatchery (Figure 73). Using PIT tags to monitor downstream movement through Lower Granite Dam, Achord et al. (1996) found that wild spring Chinook migrated later, wild summer Chinook migrated earlier, and both types migrated over a more protracted period compared to their hatchery-reared counterparts. The combined effect of hatchery-reared juveniles arriving in the estuary within an abbreviated and artificial migration window and at elevated numbers increases the density of juveniles and may artificially limit the productive capacity of the estuary.

Conclusions

Our evaluation of past and present salmon size distributions and migrations are consistent with the hypothesis that life history diversity in the estuary has declined. Despite the obvious limitations of the available estuarine data, the results of several surveys from a similar estuary location provide a valid comparison before and after intensive development modified the Columbia River basin. These results reflect the kinds of changes that might be expected based on our conceptual framework (see the "Conceptual Framework for Evaluating Estuarine Habitat Conditions" section, page 21), large-scale changes in watershed conditions, and the results of

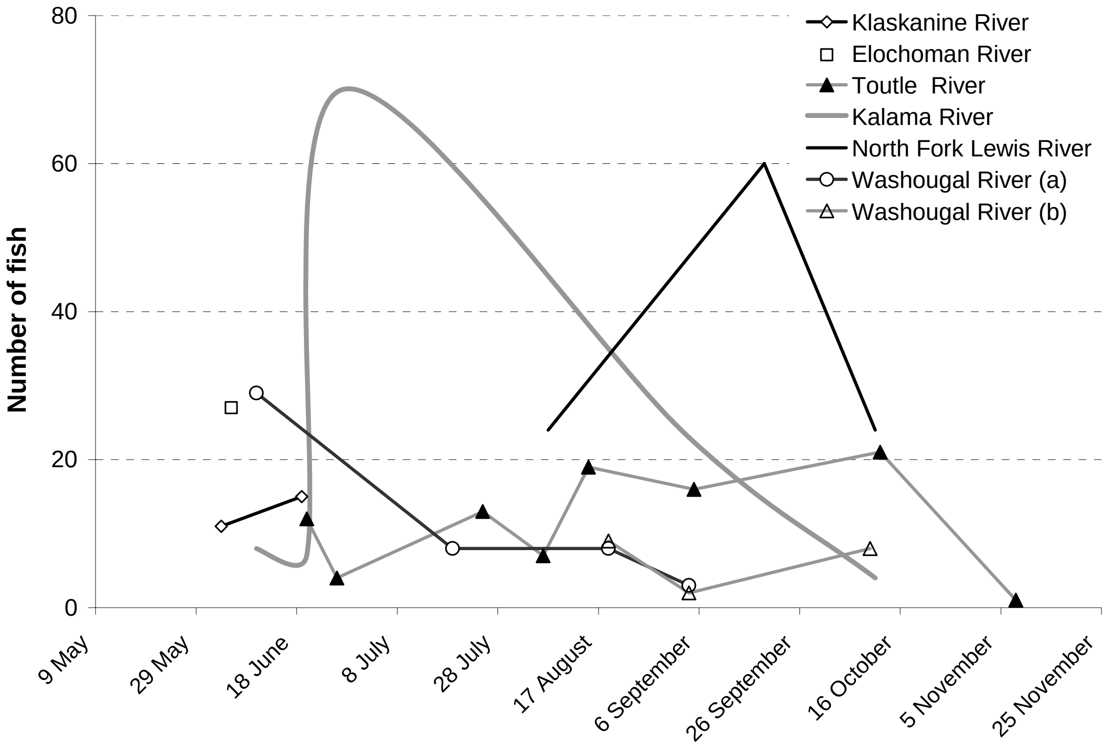

Figure 84. Time and relative duration of subyearling Chinook outmigration from six tributaries into the Columbia River estuary during 1963 (Reimers and Loeffel 1967). Two sites were sampled in the Washougal River, (a) was at the Highway 830 bridge and (b) was 10.8 miles upriver from the Highway 830 bridge.

upriver assessments that also document reduced life history diversity in the basin (Lichatowich and Mobrand 1995, ISG 2000, Williams in press). The results suggest a more uniform size distribution among subyearling estuarine migrants, relatively constricted migration periods dictated by the timing of hatchery releases, and evidence of apparently shorter estuarine residence times compared to the early results of Rich (1920).

The physical conditions of the watershed and the salmon populations when Rich (1920) studied estuarine use and residency already were modified by development and intensive fisheries. It is expected that greater diversity existed prior to his survey. Estuarine habitat for salmon has declined further since Rich (1920) sampled. We also have experienced a marked decline in wild populations, including the extinction of complete salmon runs, such that artificially propagated fish dominate present-day monitoring efforts and population-strength indicators. It is difficult to establish the importance and duration of estuarine residency by wild juvenile salmon under present conditions of reduced estuarine habitat and the predominance of hatchery-reared salmon. Multiple factors may account for the apparent reduction of small ocean-type migrants in the estuary, including:

- loss or deterioration of upriver and estuarine habitats that historically supported salmon with ocean-type life histories,

- flow modifications that have dampened established disturbance regimes and altered estuarine habitats, and
- genetic selection associated with intensive fisheries (Figure 85).

Such changes are further amplified by hatchery programs that concentrate the time of salmon entry into the estuary and further accentuate larger subyearling and yearling life histories. By releasing large batches of similarly sized fish over restricted time windows, hatcheries may limit the timing of estuarine migrations, narrow the range of habitats selected by juveniles, and artificially elevate fish densities within the estuary.

A reduction of the life history diversity or the habitats that those life histories depend upon can have implications for the overall population. Anderson and Hinrichsen (1996) argued that a hatchery population with a concentrated migratory period in the estuary would succumb to greater fluctuations in abundance because of decreased chances of encountering conditions favorable for survival. In the Columbia River, wild Lewis River ocean-type juveniles epitomized the hypothetical scenario proposed by Anderson and Hinrichsen (1996) whereby the longer migration period of the wild juveniles through the estuary may contribute to higher survival rates than their hatchery-reared cohorts (McIssac 1990). This example demonstrates factors upriver influencing migration timing to the estuary potentially affecting survival. It is critical, therefore, to document the spatio-temporal complexity of a population's life histories to understand its vulnerability and fluctuations in abundance.

Estuarine restoration activities should not be planned independent of riverine restoration efforts since habitat opportunities, life history diversity, and spatial structure of juvenile salmon in riverine habitats largely determine estuarine patterns (Healey and Prince 1995, Wallace and Collins 1997). Salmon population management and recovery efforts should promote the expression of juvenile life histories by expanding habitat opportunities (Healey and Prince 1995) in riverine and estuarine habitats. Research in Oregon's Salmon River estuary has demonstrated that marsh restoration can increase life history variation in a fall Chinook salmon population by allowing greater expression of estuarine-resident behaviors (Bottom et al. 2005).

The most vulnerable life histories to estuarine habitat losses may be the smaller ocean-type migrants (i.e., fry) that depend primarily on the upper tidal freshwater reaches (Kjelson et al. 1982, Wallace and Collins 1997). Fry migrants less than 60 mm are just one of many ocean-type life histories that contributed to the returning adult population, and one of many that depend on estuarine habitats. The survival of juveniles has been linked to estuarine habitat conditions (Magnusson and Hilborn 2003). Thus restoration of estuarine habitats in conjunction with recovery of the life histories that use those habitats will play a critical role in wild salmon recovery. This may be particularly true in estuaries of unsheltered coastal basins in California, Oregon, and Washington where salmon require additional growth before migrating to the ocean compared with populations that can migrate to the protected bays of Washington's Puget Sound and British Columbia river systems.

Unfortunately, Chinook salmon life history timing and rearing patterns have been characterized in very few river systems, our understanding of estuarine habitat use is limited in scope, and relatively few studies have investigated estuarine residency. These data are clearly needed to support salmon monitoring, management, and recovery.

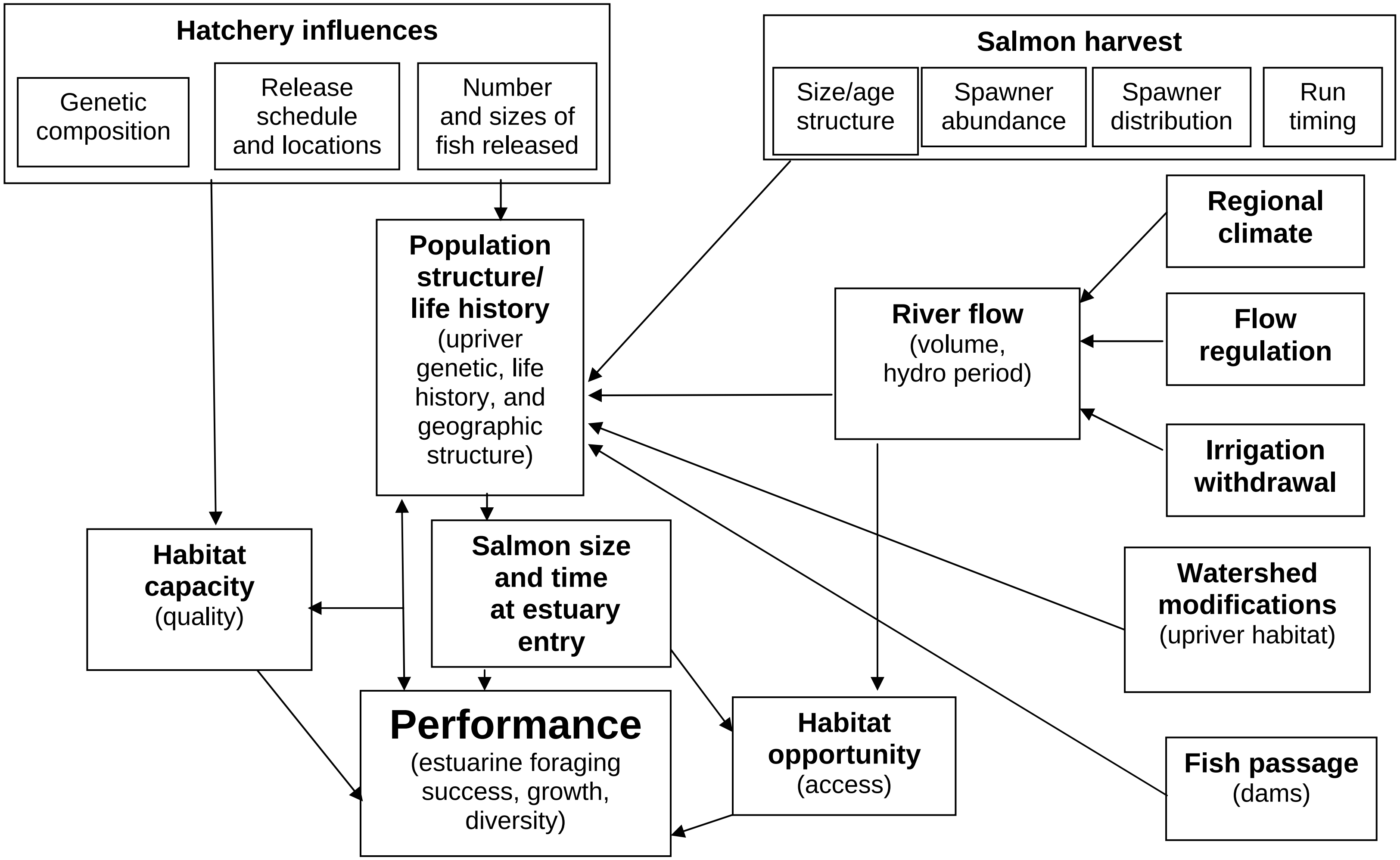

Figure 85. Linkages to life history and geographic structure of salmon populations upriver affect salmon performance within the estuary. The basin-wide geographic and genetic structure of populations may determine whether salmon can fully realize the habitat opportunity and habitat capacity in the estuary.

These results reinforce a central theme of our conceptual approach: the life histories and performance of salmon in estuaries cannot be dissociated from those of other life stages. Restoration projects to improve estuarine habitat opportunities for ocean-type juveniles, for example, may require concomitant habitat or flow improvements that can also sustain these subyearling migrants upriver. Efforts to stabilize the environment to create optimum survival conditions for one salmon life stage, however, also may reduce the variety of rearing and migration behaviors present in the population, narrowing the temporal or spatial range of habitat opportunities that salmon can potentially exploit at subsequent stages. Ironically the member/vagrant hypothesis predicts that manipulations to maximize the production of one salmon life history type upriver also may limit the total productive capacity of the estuary.

Synthesis: Review of the Conceptual Framework

Introduction

At the start of this review, we noted that traditional assumptions of natural-resource management have contributed to the decline of Columbia River salmon. More specifically, an agricultural tradition in fisheries conservation, which we described as production thinking, took for granted that salmon abundance could be maximized by eliminating mortality during critical early life stages perceived as bottlenecks to production. For every additional egg, fry, fingerling, or smolt that survived by controlling local predators, competitors, or other perceived constraints, production thinking assumed that another adult salmon would return to fishermen or the spawning grounds. Viewed through a production lens, the estuary became the last in a series of hazardous places—the lowermost end of a long river pipe—where judicious control was deemed necessary to ensure the safe and efficient flow of fish to sea.

While efforts to remove production constraints unfortunately failed to restore Columbia River salmon, it also yielded little understanding of the conditions that salmon need to persist in their native habitats. We concluded that a comprehensive review of the estuary's role in salmon decline and recovery must begin from a different conceptual framework.

In the "Conceptual Framework for Evaluating Estuarine Habitat Conditions" section (page 21), we proposed an alternative framework based on the population thinking of Rich (1939) and the member/vagrant hypothesis of Sinclair (1988). This approach emphasizes the geographic structure of habitats, populations, and diverse salmon life histories that contribute to salmon resilience and productivity. Now we briefly summarize the evidence regarding the validity of the member/vagrant hypothesis as adapted to Pacific salmon and the implications for conservation of salmon and their habitats in the Columbia River estuary.

Evidence

Geographic Structure

A central tenet of Sinclair's (1988) member/vagrant hypothesis is that population pattern and richness depend on the number of geographic settings that each species can use to complete its life cycle. The geographic structuring in populations, for example, is most evident during adult and early juvenile stages, when populations of many pelagic marine species segregate into discrete spawning/larval retention areas, or adult salmon return to their natal streams to deposit their eggs in the gravel (Sinclair 1988). Beyond just the stream environment, we applied the idea of geographic structuring to the entire habitat chain that supports salmon life cycles and that allows expression of diverse life histories within salmon populations. Each life history represents an alternative habitat pathway in time and space (i.e., geographic setting) by which population members can complete their life cycles.

Our results provide evidence that the Columbia River estuary affords a variety of alternative pathways that contribute to the geographic structure and diversity of salmon populations and life histories throughout the basin. Historic surveys indicate that Chinook salmon occurred in the estuary year-round and exhibited a wide range of times and sizes of downstream migration and periods of estuarine residency (Figure 79, Rich 1920).

Patterns of habitat use within the estuary appear to be size-related, such that small salmon migrants often rear for extended periods in shallow, nearshore habitats while larger individuals and older-age migrants tend to frequent deeper channels. Although we identified multiple factors that might contribute to the apparent decline in the proportion of fry and small fingerlings in the estuary today relative to the early 20th century (Figure 79), the response is nonetheless consistent with expectations (of the member/vagrant hypothesis) following widespread removal of shallow estuarine wetlands that allow expression of estuarine-resident life histories.

The geographic structure of spawning populations across the Columbia River basin and associated travel distances from natal streams contribute to the diverse sizes and times of juvenile migration, estuarine entry, and other life history traits in the estuary (Rich 1920). Among contemporary populations, a coarse geographic structure linked to estuarine rearing behaviors is apparent: individuals with stream-type life histories predominate in Columbia River headwaters and in Snake and Salmon rivers subbasins, while ocean-type migrants are abundant in lower Columbia River reaches.

Yet this is an oversimplification of spatial structure based on observations made long after habitat and population losses had altered historic patterns. Even contemporary life history patterns reveal a much finer geographic structuring than simply upper versus lower Columbia River basin. A population within a single watershed, for example, may exhibit stream- and ocean-type life histories. Additional work is needed to understand the population-specific linkages of Chinook salmon to diverse rearing behaviors in the estuary.

Habitat Linkages

The member/vagrant hypothesis indicates that ecological processes regulating marine population dynamics become linked across distant environments through the physical transport and migrations of species with complex life cycles (Sinclair 1988). We found evidence of significant physical and biological linkages upriver that influence salmon performance within the Columbia River estuary.

For example, flow regulation by mainstem dams controls the quantity and quality of tidal floodplain and wetland habitat accessible by young salmon; hatchery operations upriver regulate the arrival times, sizes, and patterns of habitat use by salmon within the estuary; and historic fisheries and loss of spawning and rearing habitat in freshwater determine the geographic structure of contemporary populations, which also affects the variety of migratory and rearing patterns that salmon potentially can express within the estuary. Thus we cannot interpret patterns of estuarine habitat use by salmon without accounting for physical and biological linkages upriver. The processes governing many such linkages today are dominated by hydropower, hatchery, and fishery management systems.

Salmon performance downstream in the coastal ocean similarly may be linked to the cumulative effects of river flow, habitat opportunity, and population structure upriver and in the estuary. Evidence of strong density gradients and enhanced biological production in the plume and frontal zone (Fresh et al. 2005) suggests a strong connection between Columbia River flows and prominent habitat features of the coastal ocean. These linkages further raise the possibility that control of the Columbia River hydrograph (Figure 28) may affect salmon habitat conditions offshore.

River and ocean circulation processes and the migrations of Columbia River salmon define a large and interconnected watershed-ocean ecosystem whose behavior is not adequately described by a few critical periods or habitats within the river, estuary, or nearshore ocean. Thus the general estuarine model proposed in Figure 10 can be viewed as a part of a larger system of habitat/life history interactions that regulates salmon populations (Figure 86). Salmon performance at one life stage and aquatic environment dictates the time, size, and physiological condition of surviving migrants and establishes broad limits for the potential performance of all survivors at each subsequent stage and environment. Salmon performance at all life stages is also regulated by large-scale disturbances that impose ecological constraints on the entire salmon ecosystem, including regional climate, flow regulation, and other anthropogenic effects (Figure 86). The performance of the entire salmon ecosystem is indicated by the diversity of habitat opportunities for salmon, the spatial structure and life histories of populations (i.e., the filling of habitat-opportunity space), and the basin-wide productivity and resilience of salmon species.

Spatial and Energetic Process

The member/vagrant hypothesis holds that losses of individuals from marine populations with complex life cycles may result from spatial or energetics processes. Whereas energetics losses involve direct mortality from predation, disease, or starvation, spatial losses result from the inability of individuals to find a mate successfully at the appropriate time and place to remain in the population (Sinclair 1988).

We defined spatial effects broadly as any factors that sever the link between habitat and salmon life history and cause population losses. These can result from habitat removal and genetic or phenotypic changes that prevent the individuals in a population from realizing existing habitat opportunities (Figure 9).

Evidence from the Columbia River estuary supports the idea that spatial losses have played a significant role in the decline of Columbia River Chinook salmon, including:

- loss of upriver habitats that historically supported populations with subyearling-migrant life histories,
- elimination of tidal floodplain and peripheral-wetland habitats that allowed expression of subyearling-migrant life histories within the estuary,

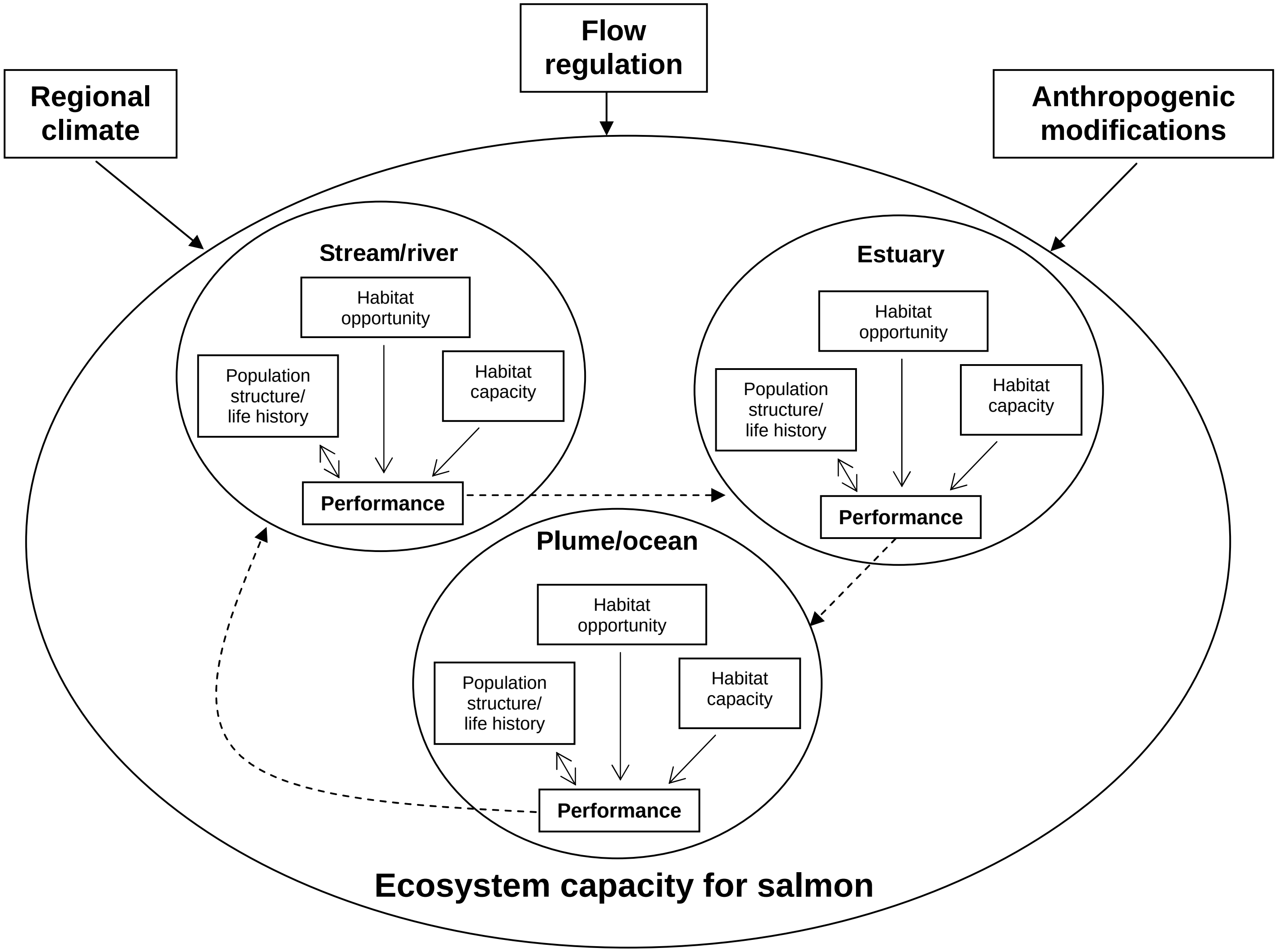

Figure 86. Linkages among salmon environments implied by the member/vagrant hypothesis (Sinclair 1998). Spatial and energetics processes shape salmon populations at each ontogenetic stage and determine the performance (growth, foraging success, and life history diversity) of the individuals that survive to enter each subsequent environment.

- effects of flow regulation on potential patterns of downstream migration by juvenile salmon, and
- genetic and phenotypic effects of hatchery programs that have concentrated the times and sizes of salmon entry into the estuary.

We also found evidence that energetics processes in the estuary may contribute to losses from Columbia River populations, including interactions with nonindigenous species, predation by marine birds, and an apparent shift from macrodetrital to microdetrital food webs. The effects of energetic and spatial processes in the estuary, however, are not easily separated.

Apparent energetic effects of recent increases in avian predation, for example, may be linked to spatial processes, including new habitat opportunities for marine birds in the lower estuary (i.e., artificial dredge-spoil islands) or changes in salmon life history linked to concentrated releases of large hatchery smolts or both. Similarly rapid increases in American shad populations could be linked to habitat changes and food-web shifts, including conversion of the free-flowing river to a series of reservoirs behind mainstem dams and related increases in microdetrital carbon sources from upriver. These examples reveal spatial-energetic interactions that are not fully depicted by the proposed conceptual model (Figure 10). Rather than independent linkages to performance, the results imply a more complex (nonlinear) dynamic among habitat opportunity, habitat capacity, and salmon life history.

Implications

Recognizing the geographic population structure within Columbia River salmon species, Rich (1939) argued for a new management approach based on the conservation of populations within their local habitats. Reviews of the Columbia River Fish and Wildlife Program (NRC 1996, ISG 2000, Williams in press) have reinforced these ideas and offered recommendations to conserve diverse salmon populations and life histories.

We conclude that the member/vagrant hypothesis offers a useful scientific framework to support such recommendations and to extend salmon recovery efforts downstream to encompass the estuarine and plume environments of salmon life cycles. This framework has significant implications for future salmon conservation and research as described in the following subsections.

Conservation Programs Must Account for Diverse Estuarine Life Histories

The results of this analysis demonstrate that neither the status of salmon populations nor the estuary's contribution to population viability is sufficiently described by simple production measures of abundance, density, and survival. Similarly the concept of single limiting factors, including the idea of a density-dependent bottleneck in the estuary, ignores the importance of spatial processes, which can play a significant role in salmon production and resilience regardless of population densities. Because spatial effects involve lost opportunities for life history expression, they cannot be measured by counting the number of live or dead fish.

Environmental fluctuations that regulate spatial processes, including interdecadal shifts in oceanic and climatic regimes, undermine production-based conservation approaches that assume the salmon ecosystem can be managed for a steady optimum condition. Population assessments and recovery plans in the Columbia River basin must account for the geographic structure and diverse life histories that allow populations to persist in a variable environment. This includes life history variations in the estuary that contribute to the geographic structure and diversity of populations throughout the Columbia River basin. This expanded view of population status is consistent with the performance criteria recently proposed by NOAA Fisheries Service to determine salmon recovery needs: abundance, population growth rate, spatial structure, and diversity (McElhany et al. 2000, Fresh et al. 2005).

Recovery Actions Should Expand Habitat Opportunity, Life History Variation

Habitat losses, hydroelectric development, salmon harvest, and fish management activities have simplified the spatial structure and diversity of salmon populations in the Columbia River basin (ISG 2000, Williams in press). Traditional salmon management programs, for example, have targeted time periods or geographic areas of maximum abundance that presumably will yield the greatest economic return. Thus rearing and release schedules for hatchery salmon are prescribed to match an average or optimal run timing, size at release, or other conditions expected to maximize survival and adult returns.

An inevitable consequence of this approach is the continued narrowing of population traits toward their mean or central tendency and an erosion of the presumably less productive tails of the distribution. In contrast, the member/vagrant hypothesis suggests that conservation programs should target the breadth of life history possibilities in an ecosystem (i.e., the full range of potential habitat/life history interactions).

Among many factors that may erode life history variation within the Columbia River estuary is the intensive hatchery propagation of large fingerling and yearling salmon, which are released over a limited range of river-flow conditions and time periods dictated by the hydropower and hatchery systems. We concluded that hatchery production and widespread habitat losses probably have narrowed the size and age distribution of Chinook salmon (Figure 79), decreasing the proportion of fry and small fingerling migrants adapted to utilize productive estuarine rearing habitats (Levy and Northcote 1982, Healey 1991).

The member/vagrant hypothesis implies that a principal goal of salmon recovery should be to expand habitat opportunities and life history expression in naturally reproducing populations. Recovery of habitat opportunities that support life history variations in the estuary offers a cost-effective strategy toward this goal. All anadromous salmonids pass through the estuary, and recovery of some estuarine habitats could simultaneously benefit multiple populations with similar life histories. Restoration of emergent and forested wetlands may be particularly important to allow expression of estuarine-resident life histories among a variety of ocean-type Chinook populations. (Bottom et al. 2005).

Reference Conditions Must Be Defined To Establish Recovery Goals

The member/vagrant hypothesis implies that present salmon distribution or standing crop in the estuary may not indicate the true rearing potential of a particular habitat. Elimination of source populations or loss of habitats elsewhere along the salmon migration route can leave otherwise suitable areas of the estuary vacant. Habitats where salmon are now most abundant might not be the highest priorities to restore or protect, if present patterns of abundance are a symptom of historic population or ecosystem decline (Li et al. 1995). Contrary to production-based conservation approaches, the goal to restore habitat opportunity requires identification of salmon life histories that are presently underrepresented and otherwise might be considered unimportant.

Long-term data sets are rarely available, and no single historic snapshot can characterize the full range of variability that existed before the estuary was intensively developed. Moreover, even if historic ecosystem conditions were known, this does not mean that all former estuarine habitats and salmon life histories can be restored. For example, increased water temperatures, stabilization of flows, or introductions of nonindigenous species might limit present habitat functions (including support of juvenile salmon) even if historic habitat form can be recreated.

The purpose of reconstructing historic reference conditions is to understand the life history variations characteristic of the species and the habitat opportunities in the basin that may have contributed to this diversity. While it may be impossible to restore former conditions, alternatives can be sought to provide equivalent opportunities for expanding life history expression.

The challenges of historical reconstruction only underscore the need to explicitly define the goals of restoration and to describe their scientific basis using whatever reference examples are available. In some situations lack of historic data may require comparisons with other, less altered populations and ecosystems to provide a benchmark for developing recovery goals.

Conserving Habitat Linkages Requires Ecosystem-scale Planning

The member/vagrant hypothesis implies that restoring selected segments of the salmon life cycle will not succeed if other links in the habitat chain are broken. Habitat assessments and salmon restoration activities in the Columbia River basin have focused primarily on the freshwater phase of the salmon life cycle. Maintaining habitat linkages throughout the salmon life cycle will require conservation planning and coordination at landscape and river-basin scales.

The effects of intensive management activities in the Columbia River basin extend far beyond the area or life stage they are meant to influence and inadvertently may alter downstream linkages in the salmon-habitat chain. We have suggested that flow manipulations intended to maximize salmon survival in the main stem also influence habitat conditions for the same fish in estuarine and plume environments. Similarly, hatchery and fish transportation programs designed to promote rapid downstream migration and improved in-river survival may narrow phenotypic variation—estuarine arrival times, sizes, and residency, for example—and thereby limit alternative survival possibilities among individuals entering the estuary and ocean. Performance criteria for management programs should account for potential effects throughout the salmon life cycle.

The member/vagrant hypothesis implies that subbasin plans also need to explicitly assess the contribution of estuarine and plume habitats to the geographic structure and diversity of upriver populations. Although the estuarine life histories of individual populations are poorly known, information for downstream migration times, sizes, and travel rates may offer clues about the estuarine habitats that are most likely to benefit local populations. Recovery plans should propose concomitant actions in freshwater, estuarine, and plume environments that are needed to support particular salmon life histories.

Strategic planning also is needed to support restoration efforts within the estuary. Many new restoration projects have been undertaken to improve and increase estuarine habitat opportunities for salmon, but site selection decisions rarely consider local project connections to the broader salmon-habitat landscape. Projects usually are chosen and implemented independently based on ad hoc funding opportunities and local landowner interest rather than strategic planning to identify the areas of greatest biological potential across the estuary landscape.

The spatial arrangement of estuarine habitats may be particularly important to salmon performance, because individuals must continually adjust their position as tidal fluctuations alter the distribution of wetted areas, depths, velocities, and chemical gradients. Access to productive estuarine wetlands, however, may require linkages to adjacent subtidal refugia so that fish can enter and exit intertidal marsh channels successfully twice daily with the tide. Restoring connections between the river and its floodplain may be particularly important throughout the tidal fresh zone of the estuary, where flow regulation and diking have eliminated access by downstream migrants. An estuary restoration plan should identify the priority areas where habitat opportunities and linkages should be restored to promote diverse estuarine life histories.

Metapopulation theory has been proposed as a framework for understanding and conserving salmon-habitat linkages in the Columbia River basin (ISG 2000, Williams in press). The theory describes regional population dynamics as a function of the spatial organization of suitable habitats and the relative rates of dispersal (straying) and extinction among local populations (Hanski and Simberloff 1996). A few empirical studies have applied metapopulation models to several inland salmonids with localized breeding and rearing areas, but no single model could explain the dynamics of inland species (Rieman and Dunham 2000).

Metapopulation models may be much more difficult to apply to anadromous salmon populations, because abundance and survival reflect processes far beyond the dispersal and extinction dynamics of local spawning and freshwater rearing habitats. While metapopulation concepts provide a valuable framework for conserving processes important to population persistence (e.g., dispersal and habitat connectivity, patch size requirements, phenotypic variation, etc., [Rieman and Dunham 2000]), the member/vagrant hypothesis may be a useful alternative to account for processes in estuarine environments that also affect the dynamics of local spawning populations.

New Research Approaches Needed

The member/vagrant hypothesis raises important scientific questions that traditionally were not deemed relevant for salmonid research in the Columbia River basin. Whereas production thinking measured salmon survival and sought methods to minimize mortality at critical life stages, Sinclair's (1988) hypothesis seeks information about habitat opportunities that allow diverse salmon populations to persist. From this perspective the member/vagrant hypothesis defines a new estuarine research agenda based on a fundamental question: What estuarine habitat opportunities and qualities are necessary to conserve the characteristic life histories and geographic structure of Columbia River salmon populations?

To answer this question, we recommend the following five types of estuarine habitat research:

Reference conditions

Historic reconstruction is needed to establish a benchmark for restoration planning in the estuary. Some historic habitat data already have been developed for the lower estuary (Thomas 1983), but similar data have not been compiled for the extensive tidal fresh region between Puget Island and Bonneville Dam. Further life history reconstruction for Chinook and other salmon species also may be possible if scale collections or other archival materials become available.

Contemporary habitat/life history associations

Additional empirical data are needed to determine the variety of salmon life histories now expressed in the estuary and the habitats that support them. Past investigations in the Columbia River estuary have examined a limited array of estuarine habitats, and little is known about the physical factors that influence habitat selection, accessibility, and performance by salmon. Scale-pattern analysis and otolith microchemistry (Volk et al. 2000, Kennedy et al. 2002) offer techniques for interpreting variations in freshwater and estuarine life history among individuals sampled in the estuary.

Habitat linkages at landscape scales

Little is known about the landscape-scale patterns of salmonid migration through the estuary or the spatial and temporal arrangement of habitats that support them. New tagging and tracking technologies often used to estimate salmon survival could be adapted to study life history variations and habitat linkages in the estuary. Although incapable of tracking the smallest individuals and life history types, new tagging technologies (PIT tags and acoustic tags) may allow comparisons of habitat use, residency, and migration behavior among a variety of salmon size classes.

Source populations for estuarine life histories

The member/vagrant hypothesis implies that salmon recovery plans should account for estuarine habitat linkages to upriver populations. The identification of distinct genetic markers among populations from different geographic areas of the basin offers one possible tool for identifying upriver sources of individuals with various estuarine life histories.

Dynamics of estuarine habitat opportunity

Habitat opportunities in the estuary continually shift through the interaction of tidal forces and river hydrology and may be sensitive to any management decisions that modify physical conditions. The preliminary results in the “Estuarine Habitat Opportunity” section (page 89) demonstrate that physical modeling may be used to evaluate alternative management scenarios based on their potential effects on the dynamics of habitat opportunity. Additional research to understand salmon-habitat associations will be needed to refine the habitat-opportunity metrics chosen for physical modeling.

Summary and Conclusions

We conclude that the member/vagrant hypothesis is a valid conceptual approach to account for the geographic structure and diversity of salmon populations that is essential to population persistence in a variable environment. The Columbia River estuary contributes to the geographic structure and diversity of populations by providing alternative rearing opportunities for upriver populations whose members arrive in the lower river at a variety of sizes and times. The evidence suggests that spatial and energetics losses affecting estuarine life histories have contributed to the decline of Chinook salmon populations throughout the Columbia River basin.

Salmon recovery programs should expand estuarine habitat opportunities to support diverse populations and life histories. This implies that multiple scales of conservation planning will be needed to account for:

1) effects of upriver management decisions (i.e., flow management, hatchery, and harvest) on salmon habitats and life histories in estuarine and plume environments,
2) estuarine habitats that support local populations or groups of populations (i.e., ESUs) throughout the basin; and
3) restoration priorities within the estuary, including the key habitat types and their spatial organization, to accommodate diverse salmon rearing and migration behaviors.

The member/vagrant hypothesis outlines a new research framework to support salmon conservation and recovery planning, including:

1) historical reconstruction of estuarine habitats and salmon life histories to establish reference conditions,
2) empirical studies to understand life history/habitat associations, to track the migrations and habitat-use patterns of various size classes of salmon, and to identify the source populations of individuals with diverse estuarine life histories; and
3) physical modeling to evaluate habitat-opportunity responses to alternative management and restoration decisions that may affect the estuary.

The member/vagrant hypothesis does not offer a specific model to define a minimum quantity or spatial arrangement of habitat that will maximize salmon abundance or ensure population viability. The complex interactions of the salmonid ecosystem described in this analysis (Figure 85 and Figure 86) demonstrate why such an optimum condition does not exist. Rather the results argue for restoring flexibility to the ecosystem by expanding habitat opportunities and life history variations and restoring the physical processes that support this diversity.

Additional work is needed to develop applications of the member/vagrant hypothesis to salmon conservation. As suggested in a review of metapopulation theory (Rieman and Dunham 2000), we conclude that the principal benefits of the hypothesis are conceptual rather than prescriptive. Applying the hypothesis to salmon recovery, regardless if its assumptions can be proven or predictive models can be developed, requires an understanding of the key processes and habitat linkages that will nudge the ecosystem in a more favorable direction toward population persistence.

Conclusions and Recommendations

Conclusions

The principal objective of this analysis was to assess the potential impact of flow regulation of the Columbia River on juvenile salmon utilization of the estuary. The analysis of historical data and hydrodynamic model simulations identified potential influences of flow regulation and of climate on hydrology and sediment transport, with likely consequences for the estuarine physical environment. Yet with the extant data it was not possible to separate or rank these effects on juvenile salmon from these compounding factors:

- anthropogenic changes to estuarine bathymetry and the tidal floodplain,
- hatchery and harvest effects on the demographics and life history diversity of juvenile salmon inclined to use the estuary,
- climate-induced variability, and
- biotic changes in the estuarine flora, fauna, and food web.

The analyses indicated that habitat and food-web changes within the estuary and other factors affecting salmon population structure and life histories have altered the capacity of the estuary to support juvenile salmon. Diking and filling activities in the estuary have likely reduced the rearing capacity for fry and subyearling life histories by decreasing the tidal prism and eliminating emergent and forested wetlands and floodplain habitats adjacent to shore. These habitats, which provide off-channel areas during peak flows, refuge from predators, and sources of macrodetrital production, probably serve different rearing functions from the other kinds of shallow habitats that model simulations suggest may have increased within the peripheral bays and other areas of the estuary.

Effects of flow regulation on habitat opportunity for subyearling salmon based on the depth criterion remain equivocal because of uncertainties in the available bathymetric data. But regardless of these modeling results, significant loss of shoreline emergent and forested wetlands that were not incorporated in these simulations could be important in limiting the productive potential of the estuary for salmon.

Despite the physical and ecological changes in habitat opportunity and capacity in the estuary, simplification of the population structure and life history diversity of salmon may be the most important factor affecting juvenile salmon performance. In the absence of data on present-day estuarine use by wild, subyearling ocean-type salmon, we concluded that patterns of salmon abundance, diversity, and residency in the modern estuary are influenced significantly by upriver habitat losses throughout the basin, harvest, and hatchery management practices.

Regulation of river flow and habitat losses in the estuary cannot independently account for apparent changes in estuarine rearing patterns of juvenile salmon. Restoration of estuarine habitats, particularly diked emergent and forested wetlands, and flow manipulations to restore historical flow patterns and habitat dynamics might significantly enhance the productive capacity of the estuary for salmon.

Regardless of the degree of habitat loss, we cannot eliminate the possibility that changes in population structure and life histories now prevent salmon from realizing the productive capacity of the estuary. Accordingly efforts to improve or to restore the estuary for salmon must be developed in concert with hatchery, harvest, and upriver habitat improvements to recover those life history types that can benefit from estuary restoration.

The results also underscore the need to establish a sound historical and evolutionary context for interpreting modern estuarine habitat conditions and for developing salmon recovery strategies. In the absence of such a context, recovery actions may inappropriately target those few salmon life history types and habitats that are abundant today, further reinforcing the symptoms of salmon decline rather than expanding the productive capacity of the basin. Continued emphasis on improving survival of a few dominant types of Chinook salmon, particularly large hatchery yearlings and fed subyearlings with short estuarine residence times, may only further narrow the sizes, times, and rates of migration, concentrating salmonid use of the estuary and preventing salmon from realizing the estuary's full productive potential.

The historical analyses suggest that just the opposite strategy is needed to improve salmonid performance: recovery efforts should expand diversity of salmon life history and habitat opportunities to allow for the widest possible range of successful rearing behaviors. Therefore efforts to improve the productive capacity of the estuary significantly for salmon may require recovery of many habitats and life histories that are now rare or nonexistent rather than those few that have come to dominate as a consequence of industrial development of the basin and intensive selection pressures from harvest and hatchery influences.

Recommendations

While the risk of extinction of many Columbia River populations implies the need for immediate recovery action, the historical lack of salmon research in the estuary argues that further study may be necessary before we can define the appropriate restorative measures. We conclude that these concerns should be addressed by initiating carefully targeted restoration activities where there is reasonable confidence in their ecological benefits and at the same time by collecting new data to better understand salmon habitat requirements and restoration needs. The following recommendations are offered as potential means to promote salmon recovery and improve estuarine conditions, as well as to advance understanding of salmon rearing requirements:

Adopt an Explicit Ecologically Based Conceptual Framework for Estuary Management and Restoration

The lack of information about the estuarine-rearing requirements of juvenile salmon is because of a longstanding production approach to salmon management and research. This approach assumes the estuary is a simple migration corridor or bottleneck, where predation and other mortality factors must be controlled, rather than a productive nursery ground, where the varied habitat needs of diverse populations and life history types must be protected. We concur with the conclusions of the Independent Scientific Group (ISG 2000, Williams in press) that a fundamental impediment to recovery efforts in the Columbia River basin is the lack of an explicit ecological framework for salmon conservation.

Such a framework is important particularly to direct recovery efforts in the estuary, where physical and biological interactions are complex and continually changing in response to tidal forces, river flows, and seasonal fluctuations in the composition of species assemblages. In addition the ecological requirements of salmon within the estuary must be placed in the broader context of factors at other life stages that shape population structure and life histories and thereby determine whether juvenile salmon can realize the full productive potential of the estuary.

The conceptual framework (member/vagrant hypothesis) adapted for this assessment provides a valid ecological approach to account for life cycle linkages that influence salmon performance in the estuary. This framework should be applied to salmon conservation:

- to identify and protect diverse salmon life histories, including variations in the estuarine rearing behaviors of subyearling migrants;
- to identify and protect the full variety of geographic features and disturbance processes in the basin that allow for diverse salmon life histories, including different patterns of estuarine rearing; and
- to establish performance criteria for evaluating whether management activities in the basin will impact salmon diversity and the productive capacity of the estuary.

Protect and Restore Opportunity for Salmon to Access Emergent and Forested Wetlands in the Estuary and Riparian Wetlands in the Tidal Floodplain

Historical losses of peripheral floodplain, wetland, and riparian habitats from diking and filling activities in the Columbia River estuary have reduced available rearing habitat for salmon with subyearling life histories. Such effects may not be limited to yearling, stream-type juveniles at present because hatcheries, harvest, and upriver habitat losses tend to favor these life histories. However, any effort to increase life history diversity will require reestablishment of important rearing habitats that have been substantially modified or removed from the estuary.

Although fish use of tidal wetlands and floodplain habitats rarely has been investigated in the Columbia River, studies in other Northwest estuaries indicate that wetland restoration could offer a cost-effective method to improve salmonid rearing conditions. Reestablishment of more natural flow regimes in the basin might also diversify estuarine habitat opportunity and its associated variety of salmon rearing and migration behaviors. The following actions are needed to support and evaluate wetland recovery projects intended to benefit salmon:

- Develop a comprehensive plan for wetland restoration throughout the tidal river and estuary, including habitat recovery objectives; criteria for site selection and restoration priorities; an inventory of diked, filled, and excavated lands; and a list of high priority sites most likely to benefit salmon recovery.

- Evaluate information on hatchery, harvest, and habitat management practices that reduce salmon life history diversity, particularly diversity of subyearling, ocean-type migrants that are potentially most dependent on estuarine habitats.
- Establish experimental restoration projects at a few representative wetland sites to evaluate the effectiveness of dike removal as a method of salmon recovery. Conduct a monitoring program at experimental and previously unaltered (undiked) reference sites to assess rates of habitat recovery, and identify conditions that affect salmonid use and performance.
- Reconstruct the historical structure of mainstem and tributary shallow-water habitat in the predevelopment tidal floodplain and compare with contemporary conditions. Evaluate the potential habitat function of this extensive area for juvenile salmon rearing and migration, and its contribution to the estuary in terms of sediment accretion and erosion, large woody debris and food-web sources, and disturbance regimes.
- Evaluate options for restoring more natural flow regimes to the estuary and assess their potential effects on estuarine habitat opportunity under a variety of different wetland-recovery scenarios and on the distribution and extent of the Columbia River plume and frontal zone.

Expand Phenotypic Diversity of Salmon, Including a Broader Range of Sizes, Times of Entry, and Duration of Residency in the Estuary

Although increased genetic and life history diversity of salmon ultimately may require long-term expansion of habitat opportunity upriver and in the estuary, rapid progress in the use of existing or restored habitats could be made by expanding phenotypic diversity of salmon now heavily influenced by hatchery programs. Such improvements could require reductions in hatchery releases or changes in hatchery rearing practices.

Any management changes to benefit salmonid use of the estuary, however, will require an improved accounting system and a greater degree of coordination of basin-wide hatchery programs than presently exists. For example, incomplete records of hatchery release groups, variations in rearing and release practices that confound interpretation of management effects, and difficulties in distinguishing the hatchery or wild origin of unmarked salmon preclude a full accounting of the influence of hatchery practices on salmon behavior and performance in the estuary. The following recommendations address these issues:

- Evaluate effects of past hatchery rearing and release practices on the sizes and times of downstream migration, estuarine residence periods, and potential densities of juvenile salmon in the estuary. Propose hatchery management alternatives for expanding the diversity of estuarine rearing behaviors and reducing the risks of hatchery programs on salmonid performance in the estuary.
- Improve accessibility of all hatchery data and accounting of all marked groups of salmon to allow future auditing of hatchery practices and their effects on the estuarine rearing patterns of juvenile salmon.

- Expand marking programs or develop alternative techniques to improve discrimination of hatchery from wild fish in the estuary. These data are critical to discern differences between the estuarine rearing behaviors of hatchery and wild fish, and ultimately to evaluate whether basin-wide salmon recovery programs are succeeding.

Monitor Variations in Life History Diversity, Habitat Use, and Performance of Juvenile Salmon in the Estuary

Because the abundance and life histories of salmon in the estuary are linked to source populations and habitats upstream, changes in life history diversity and the relative proportions of wild juveniles in the estuary may indicate whether recovery efforts throughout the basin are having a positive effect. Unfortunately there has been no long-term monitoring program to describe trends in salmon rearing behaviors in the estuary. Neither salmon scales nor otoliths have been collected or archived routinely to evaluate changes in estuarine life history patterns since Rich's survey in 1914–1916.

Most contemporary estuarine studies are of short duration, including numerous local impact studies, and only rarely have studies sampled many of the shallow habitats typically preferred by smaller subyearling salmon. The most consistent monitoring in the estuary has emphasized the migration rates and survival of large, hatchery-tagged fish, and poorly represents wild, ocean-type species and life histories that are likely most dependent upon estuarine conditions. A more representative sampling program is needed to monitor variability in the estuarine life histories and performance of salmon. Such a program should include these objectives:

- Monitor fish use of a variety of potential rearing habitats to assess variability and causal relationships affecting size characteristics, residence times, growth, and habitat use among hatchery-reared and wild salmonids.
- Initiate intensive studies of the spatial and temporal distribution, abundance, and ecology of subyearling, ocean-type juvenile salmon in selected shallow-water habitats of the estuary. Document variability in life history diversity in their use of emergent and forested wetlands.
- Identify upstream sources and freshwater histories of fish captured in the estuary through mark and tag recovery and DNA, scale, and otolith analyses. Initiate in-depth life history studies based on analyses of existing or new materials including scales or otoliths.
- Investigate patterns of movement and migration through the estuarine gradient, from tidal freshwater through brackish and estuarine habitats in different regions of the estuary.
- Compare patterns of estuarine wetland use by juvenile salmonids in the Columbia River with those in the Fraser River in British Columbia as a method for further evaluating flow regulation and hatchery influences, which are much greater in the Columbia system.

Review the Scientific Basis for Proposed Habitat and Bathymetric Changes in the Estuary Relative to the Restoration Goals of the Columbia Basin Fish and Wildlife Program

Habitat changes and economic activities within the estuary have been evaluated independently of management or restoration efforts that affect salmon and their habitats elsewhere in the Columbia River basin. The potential effects, for example, of ongoing or proposed estuarine dredging, spoil disposal, or habitat restoration activities on the Columbia Basin Fish and Wildlife Program have not been explicitly evaluated.

Because all anadromous salmonids in the Columbia River pass through or rear in the estuary before migrating to the ocean, changes in estuarine conditions could determine the effectiveness of salmonid recovery efforts throughout the basin. Modeling results show that estuarine habitat opportunity for salmonids is sensitive to bathymetric change. In addition the response of predacious birds to dredge-spoil islands artificially created and maintained in the lower estuary illustrates that at least some estuarine habitat changes may have unexpected ecological consequences.

Despite these risks, impact assessments associated with dredging and disposal activities usually have focused on localized impacts and have not considered salmonid responses to changes in habitat opportunity or capacity at a landscape scale. Nor have they considered the history of incremental change upon which each new project is superimposed or the broader responses of the ecosystem to physical habitat modifications. Thus an independent scientific review is recommended to evaluate the following:

- the scientific assumptions of Columbia River dredging and disposal programs relative to the goals and conceptual framework of the Columbia Basin Fish and Wildlife Program;
- the potential effects of historical changes in bathymetric profile on the distribution and availability of salmonid habitat and, in particular, the estuary's capacity to support a diversity of salmon life histories; and
- the significance of dredge disposal activities as a factor in estuarine habitat and ecosystem change that could affect the performance of juvenile salmon.

Use Physical Observations and Hydrodynamic Modeling to Assess the Effects of Bathymetric Change, Flow Regulation, and Alternative Restoration Designs on Habitat Opportunity

Our modeling methodology has proven to be a useful approach for evaluating the relative effects of flow modification and bathymetric change on habitat opportunity for salmon. Its present application, however, is limited by several critical data gaps, including the lack of present-day, high resolution bathymetric data and physical observations for shallow regions of the estuary. For example, the ability of the model to characterize physical habitat opportunity relative to the depth criterion (much more so than opportunity determined with respect to the velocity criterion) was very sensitive to assumed bathymetric configurations in the shallow areas of the estuary. This emphasizes the need to obtain accurate bank-to-bank bathymetric data for the lower river and estuary if there is to be an improved understanding of the impacts of river flow on physical habitat opportunity. The following activities are recommended:

- Revise historical bathymetric data and acquire new data on present-day, shallow-water bathymetry and circulation processes to resolve the lack of confidence and robustness in model predictions of habitat opportunity, especially those based on the depth criterion.

- Conduct new simulations that include three-dimensional modeling of salinity intrusion and stratification as a third environmental variable (in addition to depth and velocity) that is an important determinant of juvenile salmon distribution and residence time. Use the model to evaluate sensitivity of the estuary to incremental physical changes associated with diking, dredging, and flow regulation and the implications of these results for future management of the estuary.
- Reexamine the results of hydrodynamic modeling to evaluate landscape connectivity and other spatial indices affecting salmon habitat opportunity between historical conditions and the modern estuary configuration.
- Conduct simulations to evaluate changes in salmon habitat opportunity for alternative restoration scenarios and a range of flow conditions.

Review Results of Estuarine Predation Studies in the Context of Salmon Population and Habitat Change

It is unclear whether the high rates of salmon predation by Caspian terns and other marine birds in the estuary is a significant factor affecting salmon recovery or an ecological symptom of other changes, including alteration of estuarine habitats, simplification of the geographic structure of salmon populations, and reduced variation in salmon rearing and migration behaviors.

High predation rates on juvenile salmonids, however, could result from replacing a broad continuum of salmon life history types with punctuated releases of large hatchery fish that are concentrated in relatively few estuarine habitats over reduced time periods. Hatchery-induced changes in surface-feeding behavior also could be a factor increasing the vulnerability of salmon smolts to predators. Emphasis on estimating predation rates alone may lead to inappropriate salmon recovery proposals unless these results are evaluated in a broader historical and ecological framework. Independent scientific assessments of salmon predation studies are needed in the Columbia River estuary to address the following objectives:

- Examine the assumptions and results of ongoing predator studies in the context of historical and present-day estuarine habitat opportunity; salmon migration, rearing, and feeding behaviors; and fish densities in the estuary.
- Review the effects of bird predators on rates of adult salmon return to the Columbia River basin.
- Recommend methods for testing alternative hypotheses to explain high predation rates, and identify what, if any, recovery measures may be appropriate.

Assess the Effects of Altered Habitats and Food Webs on the Capacity of the Estuary to Support Juvenile Salmon

Results of this review indicate that a variety of ecological changes may have affected the capacity of the estuary to support wild subyearling Chinook salmon. These changes include loss of floodplain and other wetland habitats, the effects of climatic changes on physical processes and estuarine food webs, interactions with an increasing number of nonindigenous species, and shifts in the timing of established patterns of river flow and salmon migrations. Unfortunately, the direction or magnitude of these ecological changes cannot be assessed from the limited empirical data available.

The effects of altering food-web sources through habitat modifications, for example, have not been directly evaluated. We also have little data to assess the effects of a two-week advance in the spring freshet because of flow regulation and a substantial delay in peak salmon migrations because of hatchery and other influences. If estuarine prey production cycles and salmon migration behaviors are adaptive, and linked to flow variations, then such changes could create a mismatch between salmon and their prey resources, reducing the productive capacity of the estuary.

Changes in the coarse and fine sediment budgets, particularly the quality of organic matter input to the system, also are poorly understood. The following research activities are recommended to evaluate the effects of modifying estuarine habitats and food webs on the salmon-rearing capacity of the estuary:

- Use natural stable isotope analyses or other methods to investigate potential food-web disruptions because of habitat loss and degradation. These losses also should be evaluated in terms of changes to estuarine physical processes, through numerical model investigations and analyses of historical and contemporary data.
- Use field studies and modeling to evaluate the potential risk imposed on salmon recovery by nonindigenous species influencing estuarine habitats and food webs supporting juvenile salmon. This should include, but not necessarily be limited to, American shad, Asian clam, purple loosestrife (*Lythrum salicaria*), and other potential nonindigenous community dominants.
- Evaluate historical and present-day relationships between flow variability, production of key salmonid prey species (e.g., *Corophium* spp.), and the timing of salmonid migrations to the estuary.
- Assess long-term human and climatic effects on sediment budgets and inputs of organic matter. Evaluate the influence of potential climatic trends and rates of sea-level rise on the feasibility of salmon recovery actions that involve estuarine habitat restoration and river-flow modifications.
- Review the scientific design and results of recent estuarine predation studies in the context of historical changes in salmon populations and estuarine habitat opportunity.

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Appendix A: Timeline for the Columbia River Basin, 1775–2000

Table A-1. Time line of historical, scientific, legal, and natural events affecting salmonids in the Columbia River basin.

Date	Historic/ scientific	Hydropower, irrigation, and navigation	Salmon	Peak flow events
1775	Bruno de Heceta, aboard the *Santiago*, sights the Columbia River, naming it the Rio San Roque		Estimated historic Columbia River salmon runs fluctuate between 11 and 16×10^6 fish, of which Native North Americans may have captured $4.5–6.3 \times 10^6$	
1776–1787				
1788	John Mears, aboard the *Felice*, encounters breakers at the Columbia's mouth			
1789				
1790	Britain gains rights to territory in treaty with Spain			
1791				
1792	American Captain Robert Gray, aboard the *Columbia Rediva,* enters the estuary and names river; Broughton maps the estuary to Point Vancouver			
1793	De Heceta maps the estuary			
1794–1799				

Table A-1 continued. Time line of historical, scientific, legal, and natural events affecting salmonids in the Columbia River basin.

Date	Historic/ scientific	Hydropower, irrigation, and navigation	Salmon	Peak flow events
1800	Major ash fall from Mount St. Helens			
1801–1803				
1804	Lewis and Clark departs St. Louis			
1805	Lewis and Clark arrive at estuary			
1806	Lewis and Clark spend winter at Fort Clatsop and return east			
1807	David Thompson starts mapping upper Columbia River			
1808–1809				
1810	John Jacob Astor forms the Pacific Fur Company, the first permanent fur-trading colony			
1811	Astor's *Tonquin* arrives; Fort Astoria constructed			
1812				
1813	North West Fur Co. buys Astoria			
1814–1817				
1818			Spring Chinook salmon harvest begins	
1819–1822				
1823			Astor Company exports pickled salmon to London	
1824				

Table A-1 continued. Time line of historical, scientific, legal, and natural events affecting salmonids in the Columbia River basin.

Date	**Historic/ scientific**	**Hydropower, irrigation, and navigation**	**Salmon**	**Peak flow events**
1825	Hudson's Bay Company establishes Fort Vancouver and Fort Coleville; disease reduces Lower Chinook Indian population to half of its historical level			
1826				
1827	Dr. John McLoughlin of Hudson's Bay Co. builds first sawmill in Pacific Northwest at Vancouver			
1828				
1829	Capt. John Dominis brings the brig *Owyhee* into the Columbia River to fish salmon and trade. During two summers in the area, they put up 50 barrels of salted salmon that sold in Boston in 1831 for $0.10 per pound.			
1830				
1831	Mount St. Helens ash fall			
1832				
1833	John Ball is first teacher at first school in the Pacific Northwest at Fort Vancouver			
1834–1835				
1836	The *Beaver*, first steamship on river, arrives at Fort Vancouver			
1837	M.C. Ewing, in *USS W.A. Talcum*, maps 90 miles upriver			

Table A-1 continued. Time line of historical, scientific, legal, and natural events affecting salmonids in the Columbia River basin.

Date	Historic/ scientific	Hydropower, irrigation, and navigation	Salmon	Peak flow events
1838				
1839	Sir Edward Beecher conducts first official survey of bar conditions in *HMS Sulphur*			
1840	Approximately 800 Euro-American settlers in Oregon country			
1841	Com. Charles Wilkes surveys estuary for the United States; *USS Peacock* wrecks on north (Peacocks) spit			
1842	W. W. Raymond builds first frame house in the region; extensive ash fall and pyroclastic eruptions from Mount St. Helens begin			
1843		Irrigation begins in watershed		
1844–1846				
1847	Oregon Territorial Legislature passes law creating pilot service; S. C. Reeves is first pilot			
1848	Oregon becomes a territory			
1849	Lt. Commander William P. McArthur and Lt. Washington A. Bartlett begin first survey of U.S. coast			Second largest spring freshet on record, measured at 31.1–34.0 × 10^3 m^3s^{-1} at The Dalles
1850				
1851	Tansey Pt. treaties with Lower Chinook Indians; only ≈8,000 native peoples survive in Columbia River basin			

Table A-1 continued. Time line of historical, scientific, legal, and natural events affecting salmonids in the Columbia River basin.

Date	Historic/ scientific	Hydropower, irrigation, and navigation	Salmon	Peak flow events
1852				
1853	Washington becomes a territory			
1854–1855				
1856	First Cape Disappointment Lighthouse is built: cost, $38,000			
1857	Mount St. Helens ash falls and pyroclastic eruptions cease			
1858				
1859	Oregon attains statehood			24.6×10^3 m^3s^{-1} spring freshet
1860–1861				
1862				26.9×10^3 m^3s^{-1} spring freshet; also 1861–1862 winter flood on Willamette River largest on record, 8.5×10^3 m^3s^{-1}, with Portland inundated twice during the winter
1863				
1864				Moderately strong spring freshet of $>21.2 \times 10^3$ m^3s^{-1}
1865				
1866		First channel dredging	George Hume and Andrew Hapgood build Northwest's first cannery at Oak Point; first intensive fishery; 272,000-lb Chinook catch	Moderately strong spring freshet of $>21.2 \times 10^3$ m^3s^{-1}

Table A-1 continued. Time line of historical, scientific, legal, and natural events affecting salmonids in the Columbia River basin.

Date	Historic/ scientific	Hydropower, irrigation, and navigation	Salmon	Peak flow events
1867			Hume and Hapgood can 18,000 cases of Chinook; fishermen earn $.15 per fish	
1868–1869				
1870			10,200,000 lb Chinook catch	
1871				24.4×10^3 m^3s^{-1} spring freshet
1872				
1873			Four canneries operating	
1874				
1875	Point Adams Lighthouse is completed		Oregonian reports on 3 March that U.S. Fish Commissioner Spencer Baird predicts Columbia River salmon fisheries will likely be depleted, like other U.S. and European fisheries, because of overfishing, dams, and habitat loss.	
1876		First scrape dredging of Columbia River entrance bar		27.2×10^3 m^3s^{-1} spring freshet
1877			Oregon and Washington legislatures approve laws to temporarily close fisheries but provide no enforcement; Oregon/Washington Fish Propagating Co., Clackamas Hatchery begins production	
1878	Fort Canby near present-day Ilwaco, Washington, is site of first life-saving station			

Table A-1 continued. Time line of historical, scientific1, legal, and natural events affecting salmonids in the Columbia River basin.

Date	Historic/ scientific	Hydropower, irrigation, and navigation	Salmon	Peak flow events
1879				
1880				25.8×10^3 m^3s^{-1} spring freshet
1881	Lt. Thomas W. Symons, USACE, maps estuary			
1882				24.9×10^3 m^3s^{-1} spring freshet; large winter flood on Umatilla River
1883	Transcontinental railroad is completed		55 canneries operating in estuary, canning 629,400 cases (catch of 42,799,000 lb Chinook), which is peak Chinook harvest	
1884				
1885		South Jetty construction begins		
1886			Columbia River Fisherman's Protective Union formed	
1887		T. M. Sullivan Dam, first dam of significant size in the system, is built on Willamette River	First regulatory board (3 members) in Oregon attempts to supervise fishery; state Clackamas Hatchery production begins	25.5×10^3 m^3s^{-1} spring freshet
1888			Last year that only Chinook were caught commercially; federal Clackamas Hatchery production begins	
1889	Washington attains statehood		Sockeye (blueback), 1,210,000 lb, and steelhead, 1,727,000 lb, begin appearing in catch; state Warrendale Hatchery begins production	

Table A-1 continued. Time line of historical, scientific, legal, and natural events affecting salmonids in the Columbia River basin.

Date	Historic/ scientific	Hydropower, irrigation, and navigation	Salmon	Peak flow events
1890			Fall Chinook harvest begins; fish commission is established in Washington; report to Oregon State Board of Fish Commissioners on juvenile loss in irrigation ditches	Second largest winter flood on Willamette River
1891				
1892			Spring and summer Chinook runs 95% of canneries; declining numbers of Chinook; first coho (283,000 lb) harvest	
1893		Snag Island dike is built; Cordell Channel flow is diverted to North Channel	Salmon price is $1.15/lb; first chum (157,000 lb) harvest; U.S. Fish Commissioner Marshall MacDonald warns Oregon Governor of "disastrous outlook for the future of salmon fisheries of the Columbia"	
1894			Fishermen's Protective Union affiliated with American Federation of Labor	Largest spring freshet on record, measured 24. × 10^3 m^3s^{-1} at The Dalles
1895		South Jetty is completed; rock ledge near Astoria is blasted	30,254,000 lb Chinook catch; state hatcheries at Chinook and Kalama, and private hatchery on upper Clackamus, begin production	
1896			Columbia River Packers' association formed	Moderately strong spring freshet of >21.2 × 10^3 m^3 s^{-1}
1897			Federal Little White Salmon and Upper Clackamus Hatcheries begin production	Moderately strong spring freshet of >21.2 × 10^3 m^3s^{-1}
1898	North Head Lighthouse is completed			

Table A-1 continued. Time line of historical, scientific, legal, and natural events affecting salmonids in the Columbia River basin.

Date	**Historic/ scientific**	**Hydropower, irrigation, and navigation**	**Salmon**	**Peak flow events**
1899		7.6-m (25 feet) navigational channel from mouth to Portland gets OK	State Wind, Wenatchee hatcheries begin production	Moderately strong spring freshet of 21.2×10^3 m^3s^{-1}
1900	American Indian population has declined by 95%, while Euro-American population has increased to 1.1×10^6	2,000 km^2 of Columbia River basin under irrigation		
1901				6.1×10^3 m^3s^{-1} winter flood on Willamette River
1902		Dredging across Upper Sands Shoal is completed; navigational channel is realigned		
1903	Dredge *Grant* arrives in estuary			Moderately strong spring freshet of $>21.2 \times 10^3$ m^3s^{-1}; 6.6×10^3 m^3s^{-1} winter flood on Willamette River
1904	Dredge *Chinook* arrives in estuary			
1905		River and Harbor Act of 1905 approves Entrance Project, including South Jetty extension		
1906	Steamships *Charles R. Spencer* and *Bailey Gatzert* race from The Dalles to Portland; the *Spencer* runs the Cascades and wins			
1907				6.0×10^3 m^3s^{-1} winter flood on Willamette River
1908				

Table A-1 continued. Time line of historical, scientific, legal, and natural events affecting salmonids in the Columbia River basin.

Date	Historic/ scientific	Hydropower, irrigation, and navigation	Salmon	Peak flow events
1909		Substantial dredging begins in estuary; Grays River channel obstructions are cleared	State Bonneville Hatchery begins production	5.5×10^3 m^3 s^{-1} winter flood on Willamette River
1910		Lower Salmon and Swan Falls Dams (Snake River) is completed	Hatcheries started rearing (feeding) fry	
1911			36,603,000 lb. Chinook catch, but marked decline noted	
1912			Spring and summer-run Chinook had dropped by 75%	
1913		Extension to South Jetty is completed; North Jetty construction begins; Cowlitz River, Oregon Slough, and Baker Bay channels are dredged		
1914	Rich's first year sampling juvenile salmon	South Jetty extension completed; extensive dredging and pile dike construction begins in river channel		
1915				
1916	Rich's last year sampling juvenile salmon			
1917		North Jetty extension is completed; 9.1 m (30 feet) channel is authorized from mouth to Brookfield		
1918–1919				

Table A-1 continued. Time line of historical, scientific, legal, and natural events affecting salmonids in the Columbia River basin.

Date	Historic/ scientific	Hydropower, irrigation, and navigation	Salmon	Peak flow events
1920		North Jetty extension completed; 9.1 m (30 feet) channel authorized from mouth to Brookfield	Harvest in obvious decline	
1921–1922				
1923				5.6×10^3 m^3s^{-1} winter flood on Willamette River
1924		Clatskanie River channel is dredged	State Klaskanine Hatchery begins production	
1925–1927				
1928		Deep River channel is cleared; 10.7 m (35 ft) river channel is recommended		
1929–1930				
1931		South Jetty rehabilitation begins; Lake River channel is dredged		
1932	USACE conducts current survey at entrance	Chinook Island pile dike is constructed		
1933		Rock Island Dam is completed		
1934	U.S. Bureau of Fisheries begins comprehensive survey of Columbia River tributaries	Ilwaco Channel is completed		

Table A-1 continued. Time line of historical, scientific, legal, and natural events affecting salmonids in the Columbia River basin.

Date	Historic/ scientific	Hydropower, irrigation, and navigation	Salmon	Peak flow events
1935		10.7 m (35 feet) Columbia River channel is completed; dikes along river are completed; Harrington Point, Multnomah, and Cathlamet channels is completed		
1936		Estimated 175 dams in Columbia River basin		
1937	Bonneville Power Administration (BPA) is established			
1938		Bonneville Dam is completed; Youngs Bay channel is cleared; North Jetty rehabilitation begins		
1939		Jetty A, North Jetty rehabilitation and Sand Island pile dikes are completed; Skipanon Channel and Westport and Elochoman sloughs are dredged	Fisheries biologist Rich predicts rapid “extermination of a large part of the remaining runs of Chinooks and bluebacks”	
1940		Chinook Channel and Astoria mooring basin and breakwaters are completed		
1941		Grand Coulee Dam completed; concrete terminal added to South Jetty		
1942				

Table A-1 continued. Time line of historical, scientific, legal, and natural events affecting salmonids in the Columbia River basin.

Date	Historic/ scientific	Hydropower, irrigation, and navigation	Salmon	Peak flow events
1943				5.9×10^3 m^3s^{-1} winter flood on Willamette River
1944		Ilwaco Channel is completed		
1945		Lois Island is created with dredged material; routine annual is dredging of entrance begins		5.2×10^3 m^3s^{-1} winter flood on Willamette River
1946	USACE initiates research on radionuclides in-river, estuary, and coastal ocean			
1947	USGS bathymetric survey of estuary and river begins			
1948		Ilwaco and three pile dikes on Sand Island are completed		Third largest spring freshet on record, the "Vanport Flood" measured 28.3×10^3 m^3s^{-1} at The Dalles
1949	Columbia River Advisory Group (CRAG) is formed to advise Hanford operations	Bliss Dam is completed (Snake River)		
1950	Flood Control Act of 1950	Astoria East Mooring Basin is completed		
1951		Desdemona Shoal Channel realignment begins		
1952		C. J. Strike Dam is completed (Snake River)		
1953		Fourth Sand Island pile dike is completed		

Table A-1 continued. Time line of historical, scientific, legal, and natural events affecting salmonids in the Columbia River basin.

Date	Historic/ scientific	Hydropower, irrigation, and navigation	Salmon	Peak flow events
1954		McNary Dam is completed; River and Harbor Act of 1954 approves 14.6-m (48 feet) entrance channel project		
1955		Chief Joseph Dam is completed		
1956				
1957		The Dalles Dam is completed; Warrenton Mooring Basin dredging and Ilwaco Channel deepening are completed		
1958		Brownlee Dam (Snake River) is completed; Westport Slough is cleared; Chinook breakwaters are extended; dredge disposal Site B becomes primary disposal area		
1959	Major USACE-supported circulation study begins	Priest Rapids Dam is completed		
1960		Cowlitz River channel is dredged		
1961		Rocky Reach Dam, and Ice Harbor and Oxbow dams on Snake River, are completed; South Jetty and Jetty A are rehabilitated		

Table A-1 continued. Time line of historical, scientific, legal, and natural events affecting salmonids in the Columbia River basin.

Date	Historic/ scientific	Hydropower, irrigation, and navigation	Salmon	Peak flow events
1962	Completion of USACE-WES physical model of estuary; Working Committee for Columbia River Studies forms to probe Hanford radionuclides	12.2-m (40 feet) Columbia River channel to RKm 169 and 18.5 km up Willamette River gets approval		
1963	USACE-WES prototype physical measurements begin	Wanapum Dam is completed		
1964				5.1×10^3 m^3 s^{-1} winter flood on Willamette River
1965	Radionuclide studies of estuary sediments			
1966	Astoria-Megler Bridge completed; radionuclide studies of Columbia River			
1967	Haertel and Osterberg publish first major scientific paper on biota of the estuary (Ecology 48:459–472)	Wells Dam and Hells Canyon Dam completed (Snake River)		
1968		John Day and Arrow Lake/Keenleyside Dams completed		
1969	Haertel et al. publish first significant scientific treatise on nutrient and plankton dynamics (Ecology 50:962–978)			
1970		Little Goose Dam completed (Snake River)		
1971				

Table A-1 continued. Time line of historical, scientific, legal, and natural events affecting salmonids in the Columbia River basin.

Date	Historic/ scientific	Hydropower, irrigation, and navigation	Salmon	Peak flow events
1972	Pruter and Alverson's "The Columbia River Estuary and Adjacent Ocean Waters: Bioenvironmental Studies" published as a compilation of USACE studies in the estuary and ocean since 1942			
1973		Mica Lake Dam and Lower Granite (Snake River) dams completed		
1974				
1975	USACE current meter studies			
1976		12.2 m (40 feet) river channel completed from entrance to Portland/ Vancouver; Oregon Slough deepened		
1977		15.9 m (52 feet) entrance project initiated		
1978	USACE current meter studies			
1979	Initiation of CREDDP investigations			
1980	Mount St. Helens erupts, massive mudflows run down Toutle River into the Cowlitz River and then into the Columbia River	31,6000 km^2 under irrigation		
1981	U.S. NOS current meter study			
1982	Coal port channel to Tongue Point proposed			

Table A-1 continued. Time line of historical, scientific, legal, and natural events affecting salmonids in the Columbia River basin.

Date	Historic/ scientific	Hydropower, irrigation, and navigation	Salmon	Peak flow events
1983		5–11 × 10^6 m^3 of material is dredged from the Cowlitz/Columbia confluence		
1984	Final CREDDP "Integration Report" published	Revelstoke Dam is completed		
1985		Total annual water withdrawal of 13,300 × 10^6 m^3		
1986–1988				
1989		Deepening of 13.1 m (43 feet) navigational channel is authorized		
1990	Five-year lower Columbia River Bi-state Water Quality Study begins		Snake River sockeye and Chinook are listed under Endangered Species Act	
1991				
1992			Snake River fall Chinook is listed as threatened under ESA	
1993				
1994		Feasibility study of dredging navigational channel to 13.1 m (43 feet) begins		
1995				
1996	With completion of Lower Columbia River Bi-state Water Quality Study, lower river and estuary become National Estuary Program site (U.S. EPA)			

Table A-1 continued. Time line of historical, scientific, legal, and natural events affecting salmonids in the Columbia River basin.

Date	Historic/ scientific	Hydropower, irrigation, and navigation	Salmon	Peak flow events
1997				Strongest spring freshet in 23 years, but only 16.2×10^3 m^3s^{-1}
1998			Upper Columbia River spring-run Chinook and lower Columbia River steelhead ESU is proposed for listing as endangered, and several mid- and lower-Columbia River Chinook ESU stocks as threatened, under ESA	
1999	National Estuary Program completes comprehensive management plan for lower river and estuary	USACE approves environmental impact statement to deepen the Columbia River navigation channel from 40 to 43 feet.	10-23 × 10^6 salmon smolts are estimated to be consumed by Caspian terns nesting on Rice Island, an artificial, dredged material disposal island in the middle of the estuary	
2000				

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