Pacific Salmon and Wildlife

Ecological Contexts, Relationships, and Implications for Management

Special Edition Technical Report

PREFACE

This Special Edition Technical Report is a product of the project: *Wildlife-Habitat Relationships in Oregon and Washington* (Johnson and O'Neil 2000). The integration of information on the ecology and management of species in terrestrial, freshwater, and marine environs has been a focus of the project since its inception. For the first time, this Special Edition Technical Report synthesizes fundamental and crucial information linking salmon with wildlife species and the broader aquatic and terrestrial realms in which they co-exist. Readers will find this scientifically-robust Report to greatly strengthen our collective understanding of the role that salmon play in the populations of Pacific Northwest wildlife species, the ecology of freshwater ecosystems, and how management activities such as hatcheries and harvest can impact these aspects.

We thank the authors who contributed important time and effort to the making of this Report. Efforts on this Special Edition Technical Report have been supported by a large number of entities, including the 33 *Project Partners* and *Contributing Sponsors* of the *Wildlife-Habitat Relationships in Oregon and Washington*:

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Additional copies of this report can be acquired by contacting Lynette Wickett, WDFW, Habitat Program, 600 Capitol Way N., Olympia, WA 98501-1091; email: *wickelaw@dfw.wa.gov*.

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Cover photo: Juvenile glaucous-winged gull feeding on chum salmon carcass. Photo by C. Jeff Cederholm. Northwest Indian artwork by Bill Martin. Cover design work by Charley Barrett.

PACIFIC SALMON AND WILDLIFE - ECOLOGICAL CONTEXTS, RELATIONSHIPS, AND IMPLICATIONS FOR MANAGEMENT

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TABLE OF CONTENTS

ABSTRACT

There are seven indigenous salmon and trout of the genus *Oncorhynchus* in Washington and Oregon (chinook, coho, chum, sockeye, and pink salmon, and steelhead and cutthroat trout), for this paper we will collectively call them salmon. Their habitat extends from the smallest inland streams to the vast North Pacific Ocean, an area of freshwater, estuarine, and ocean habitats in excess of 4 million km^2. Due to past commercial fisheries, habitat loss, hatchery problems, and more recently a changing ocean environment, salmon populations have shown substantial decline over the past several decades. Many salmon stocks in Washington and Oregon are now listed as either threatened or endangered, under the Federal Endangered Species Act.

Early in this century and up until relatively recently, commercial fishing permanently diverted massive quantities of nutrients away from Washington and Oregon rivers, and their respective fish and wildlife inhabitants. Recent calculations by Gresh et al. [174a] indicate that only 3 percent of the marine-derived biomass once delivered by anadromous salmon to the rivers of Puget Sound, the Washington Coast, Columbia River, and the Oregon Coast is currently reaching those streams. There have also been many other losses of salmon habitat during this period caused by: river channel clearing and channelization, log driving and splash damming, extensive land clearing, major water diversions, livestock grazing, mining runoff pollution, logging road associated erosion and removal of the old growth forest, filling and diking of wetlands and estuaries, hydroelectric dam development, urban runoff, water and sediment contamination with toxicant, and recently recognized human induced oligotrophication of waterways. Over fishing and habitat degradation, together with a background of a changing ocean environment, have cumulatively reduced stock resilience. A century of hatchery programs have failed to rebuild the wild runs, and in many cases, likely contributed to their further declines. Modern salmon management techniques have become highly sophisticated, however, they have not been able to keep pace with the salmon population declines.

The life history of anadromous salmon covers time spent in freshwater, estuaries, and the ocean. Freshwater habitats are mainly used for spawning, incubation and juvenile rearing; estuaries are where juveniles put on critical rapid growth and make important osmoregulatory adjustments as they transition between fresh and saline waters; and the ocean is where significant feeding results in most of the body mass of the returning adults. Throughout their life salmon feed on a wide variety of prey organisms, including many kinds of freshwater and marine invertebrates and fishes; and at the same time, are fed upon by a wide variety of invertebrate and vertebrate predators and scavengers.

Juvenile salmon are known to feed directly on salmon carcass flesh, salmon eggs, and aquatic macroinvertebrates that may have previously fed on salmon carcasses. Research has uncovered significant contributions of nutrient from spawning salmon to the collector-gatherer macroinvertebrate community. Caddisflies, stoneflies, and midges are involved in processing the microbially conditioned salmon carcass flesh. Increase in aquatic macroinvertebrate density from the introduction of salmon carcasses stimulates feeding by early life stages of select salmon species. Other stages of the salmon life cycle also contribute to the macroinvertebrate food base,

such as some stonefly nymphs, when they scavenge dead pink and chum salmon embryos and alevins within the gravelbed.

A recent study of consumption of salmon by vertebrate wildlife found that 138 species of birds, mammals, amphibians, and reptiles were predators or scavengers of salmon at one or more stages of the salmon life. Of this group of wildlife species, 9 species had a *Strong-Consistent* relationship, 58 a *Recurrent* relationship, 25 an *Indirect* relationship, and 65 had a *Rare* relationship (the tally is more than 138 because 19 species have more than one type of relationship with salmon). These species were further examined as to the life cycle stage of salmon to which they were linked. The five salmon life stages, and the number of wildlife species associated with each (in parenthesis) were: *Incubation* (23); *Freshwater Rearing* (49); *Saltwater* (63); *Spawning* (16); and *Carcasses* (83) (this tally of wildlife species totals more than 137 because 66 species of wildlife are associated with salmon at several life stages).

Salmon act as an ecological process vector, important in the transport of energy and nutrients between the ocean, estuaries, and freshwater environments. The flow of nutrients back upstream via spawning salmon and the ability of watersheds to retain them plays a vital role in determining the overall productivity of salmon runs. As a seasonal resource, salmon directly affect the ecology of many aquatic and terrestrial consumers, and indirectly affect the entire food web. The challenge for salmon, wildlife, and land managers is to recognize and account for the importance of salmon not only as a commodity resource to be harvested for human consumption, but also for their crucial role in supporting overall ecosystem health. It is also important that naive view of wildlife as only consumers of salmon be abandoned. Many species of wildlife for which hard earned environmental laws and significant conservation efforts have been established (e.g., grizzly bears, bald eagles, river otters, killer whales, beaver), play key roles in providing for the health and sustainability of the ecosystems upon which salmon depend. As the health of salmon populations improves, increases in the populations of many of the associated wildlife species would be expected. Salmon and wildlife are important co-dependent components of regional biodiversity, and deserve far greater joint consideration in land-management planning, fishery management strategies, and ecological studies than they have received in the past.

Most measurements in this text are in metric system, however, conversions to English are given in Table 1.

Table 1. Metric to English Conversions.

Metric	**English**	**To Convert From Metric to English Multiply Metric by:**
millimeter (mm)	**inch (in)**	**0.039**
meter (m)	**feet (ft)**	**3.281**
square kilometer (km^2)	**square mile (mi^2)**	**0.386**
kilometer (km)	**mile (mi)**	**0.621**
gram (g)	**ounce (oz)**	**0.035**
kilogram (kg)	**pounds (lbs)**	**2.205**
cubic meter (m^3)	**cubic yard (yd^3)**	**1.308**
metric ton (mt)	**ton (t)**	**1.102**

INTRODUCTION

The landscapes of Washington and Oregon at first glance appear to have some disconnect between the terrestrial and ocean environments. Yet, abundant rivers and streams flow from the interior to the coastal zones, actively connecting the freshwater, estuarine, and ocean systems. Within these environments there are countless abiotic and biotic processes which form a highly integrated ecosystem.

Plate #1. The White River flowing from Mt. Rainier, WA. (Photo by: Larry Dominquez)

Key inhabitants include wild anadromous Pacific salmon (*Oncorhynchus* spp.) (anadromous fishes are those that spend much of their lives feeding in the ocean and migrate to freshwater to breed), 605 identified common vertebrate wildlife species, and numerous species of macroinvertebrates and other fishes. Complex relationships have evolved within and between anadromous salmon and these inhabitants that may be important for maintaining this ecosystem. Past highly exploitive fisheries, poor land use practices, an over-reliance on salmon hatcheries, and a changing ocean environment, have all contributed to many salmon stock declines in these states [367]. It has been suggested that future salmon conservation will need to take an ecosystem approach if wild stocks are to survive [485]. The purpose of this paper is to identify known relationships between wild salmon and wildlife, discuss the ecological context of these relationships, and to suggest new ways of managing the salmon resource with an ecosystem perspective in mind.

We define wild salmon as indigenous species that are the progeny of streambed spawners. This definition is used to distinguish wild salmon from hatchery (artificially) propagated salmon. The genus *Oncorhynchus* includes both salmon and trout, however for our purpose we collectively refer to them simply as salmon. Wildlife are divided into two main categories, indigenous macroinvertebrates (aquatic and terrestrial) and vertebrates (amphibians, reptiles, fishes, birds, and mammals) found in Washington and Oregon.

It is important to recognize that the ecosystem of Washington and Oregon salmon can be hemispheric in scale; reaching from local inland watersheds, where spawning occurs, all the way to ocean feeding grounds north of the Aleutian Islands of Alaska, west to the Asian side of the Pacific Ocean, and back again. This ecosystem spans an area of freshwater and ocean habitat in excess of 4 million km^2. The essence of the salmon is that it links together what humans generally consider distant, diverse, and separate ecosystems,

Plate #2. Indian fishing for salmon at Celilo Falls on the lower Columbia River. (Photo by: Archive of The Spokesman Review, Spokane, WA).

and relatively long time spans.

Scientific knowledge of salmon in Washington and Oregon was preceded by a rich legacy of aboriginal culture, which wove them into everyday life [98, 431, 379]. Salmon were an important food staple and a basis of many legends of the native people of these states, particularly those that lived along rivers and marine areas. Salmon were consumed by natives in large quantities, for example, Craig and Hacker [109 cited in 379] calculate that pre-contact catches of salmon in the Columbia basin alone ranged between 4.5 and 5.6 million fish annually. Most of the salmon caught at that time were consumed within their respective river drainage and some were traded with distant tribes. Columbia River tribal records indicate that salmon were transported long distances inland, including trade routes over the Continental Divide.

"*The Wishram and Wasco (tribes along the lower Columbia River near Celilo Falls) seem to have been the focal point in the most extensive trade network in the plateau -- one that reached to the mouth of the Columbia and out onto the plains east of the Rockies. They traded dried fish (salmon) for bison hides and other commodities that originated on the plains*." [177 cited in 379]. Some of the earliest Euro-Americans to view Pacific salmon traveled to the Northwest with the Lewis and Clark expedition in 1805. Near the confluence of the Columbia and Snake rivers, they observed salmon in unimaginable abundance: "*The number of dead Salmon on the Shores & floating in the river is incrediable* (sic) *to say....*" [William Clark in 1805, p 252 cited in 119].

European settlement and commercial development of Washington and Oregon brought significant habitat problems for the salmon; resulting in many physical, chemical, hydrological, and biological modifications to the environment. Varied effects on salmon habitat are often interrelated in complex ways and the effects of various activities and ecosystem modifications can be cumulative [513]. Some of the more harmful habitat losses caused by man have been: river channel clearing and channelization, log driving and splash damming, extensive land clearing, major water diversions, livestock grazing, mining runoff pollution, logging road associated erosion and removal of the old growth forest, filling and diking of wetlands and estuaries, hydroelectric dam development, urban runoff, water and sediment contamination with

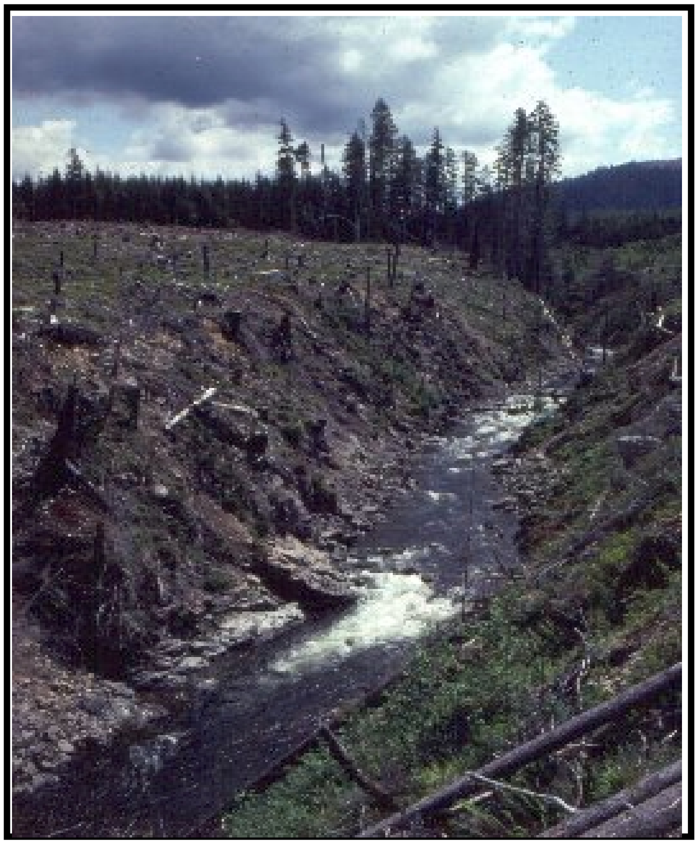


Plate #3. Clearcut logging along Matheny Creek, Washington. (Photo by: Jeff Cederholm).

toxicants, and recently recognized human induced oligotrophication of waterways [208, 296, 101, 245, 453, 485, 365, 174, 59, 16, 543].

Fishery exploitation of Columbia River salmon by Euro-Americans became a major factor after the middle to late 1800s. To ensure primary access to the salmon, commercial fisheries were strategically located downstream of popular Indian fishing grounds. The principle means used to catch the salmon were

Plate #4. Urbanization and habitat loss in the Puyallup River estuary and floodplain, Tacoma, Washington. (Photo by: Washington Department of Natural Resources Photo and Mapping section).

Plate #5. Grand Coulee Dam, an impassable hydroelectric dam on the Columbia River, Washington. (Photo by: Larry Dominguez)

gillnets, traps, seines, and fish wheels [121, 458, 274]. It was reported that "...on a single spring day in 1913 the Seufert brothers' wheel no. 5 turned a record catch of 70,000 pounds" [103]. After the 1870s and up to the early 1900s, the Columbia River salmon fishery grew from 1 to 40 canneries [478, 368 cited in 365].

Fish wheels were prohibited on the Columbia River after 1935 [365]. Commercial landings of Columbia River salmon and steelhead peaked between 1880 and 1930, and then went into a long term decline up to present times [365]. Depletion of the prime spring and summer chinook probably started earlier however, as the fishery shifted to the less desirable coho and fall chinook [275]. One estimate of annual pre-Euro-American salmon and steelhead run size for the Columbia River ranges between 8.2 and 16.3 million fish [379].

Early attempts to increase salmon catches using salmon hatcheries began as early as the 1870s, when concerns about over fishing led the Oregon and Washington Fish Propagating Company to construct a salmon-breeding station on the Clackamas River [365]. By the 1960s, with the advent of the

Plate #6. Fish wheel scow on the Columbia River at the Cascades, loaded with blueback (sockeye) salmon, c. 1895. (Photo by: Oregon Historical Society: OrHi-214, reproduction number 340)

Plate #7. Salmon Catch at the Seattle Wharf. (Photo by: Washington State Historical Society, Tacoma, WA. Negative No. 1994.123.121)

Oregon Moist Pellet medicated food, hatchery salmon production increased dramatically. Total annual Columbia-Snake River system hatchery production (Washington, Idaho, and Oregon) reached 216 million smolts in 1989 [390]. The catches of salmon in the Columbia River fisheries in these times were high relative to recent times; however, they were largely hatchery fish. In the early 1990s about 95% of the coho, 70% of the spring chinook, more than 50% of the fall chinook, more than 80% of the summer chinook, and 70% of the steelhead production in the Columbia-Snake River system were of hatchery origin [390]. By the middle 1990s there were well over 100 state, federal, tribal and private salmon hatcheries in Washington and Oregon. With the increasing reliance on artificial propagation, concerns became greatly heightened that contemporary hatchery programs were having negative effects ont he genetic diversity and persistence of

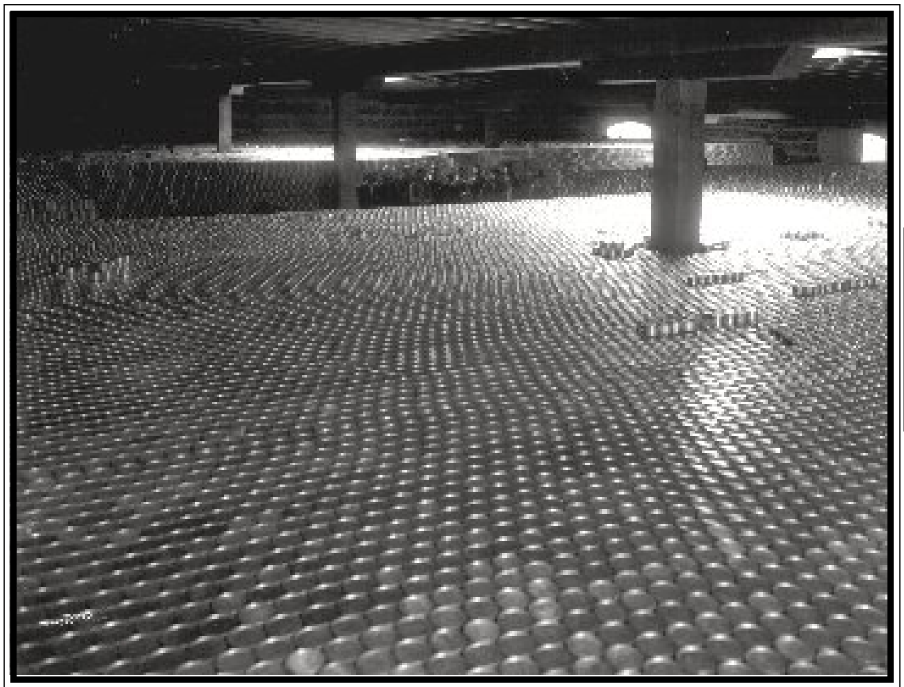


Plate #8. Canned salmon at the Apex fish company (1913). Photo by: Curtis. Washington State Historical Society. Negative No.27683.

wild populations, and that increasing releases of hatchery fish could not override other factors contributing to the overall decline of salmon [307, 365]. The history of artificial propagation reveals a recurring cycle of technological optimism followed by pessimism.

While many attempts have been made at remedying the threats of habitat loss, over fishing, and hatchery impacts, they have not been enough to prevent the widespread decline of wild salmon stocks in these states. Recent publications have chronicled the low abundance of wild salmon stocks along the Pacific Coast in the lower 48 states [367, 53, 542, 387, 181]. In 1991, the American Fisheries Society [367] published a list of 214 naturally spawning stocks of salmon, steelhead, and cutthroat from California, Oregon, Idaho, and Washington, including: 101 stocks at high risk of extinction, 58 at moderate risk of extinction, 54 stocks of special concern, and one classified as threatened under the Federal Endangered Species Act (ESA) of 1973. Fifty-eight of these stocks occur along the Oregon coast, 41 along the Washington coast and in Puget Sound, and 76 within the Columbia River basin. In spite of past salmon habitat degradation and over fishing, however, some stocks remain healthy [221]. Since 1990, the National Marine Fisheries Service (NMFS) has received a number of petitions to list Pacific salmon stocks as threatened or endangered under the ESA, and the first salmon stock of this area to be listed as endangered was the Snake River sockeye, in November 1991 [366a].

GENERAL SALMON LIFE HISTORY

There are seven species of Pacific salmon and trout of the genus *Oncorhynchus* in Washington and Oregon, and they include: chum (*O. keta*), pink (*O. gorbuscha*), sockeye (*O. nerka*), chinook (*O. tshawytscha*), and coho salmon (*O. kisutch*); and rainbow (called steelhead when anadromous) (*O. mykiss*) and coastal cutthroat trout (*O. clarki clarki*). Some of these species, including the sockeye salmon (kokanee) and rainbow and cutthroat trouts, have both anadromous and nonanadromous forms. Salmon life history patterns follow a basic theme (Figure 1).

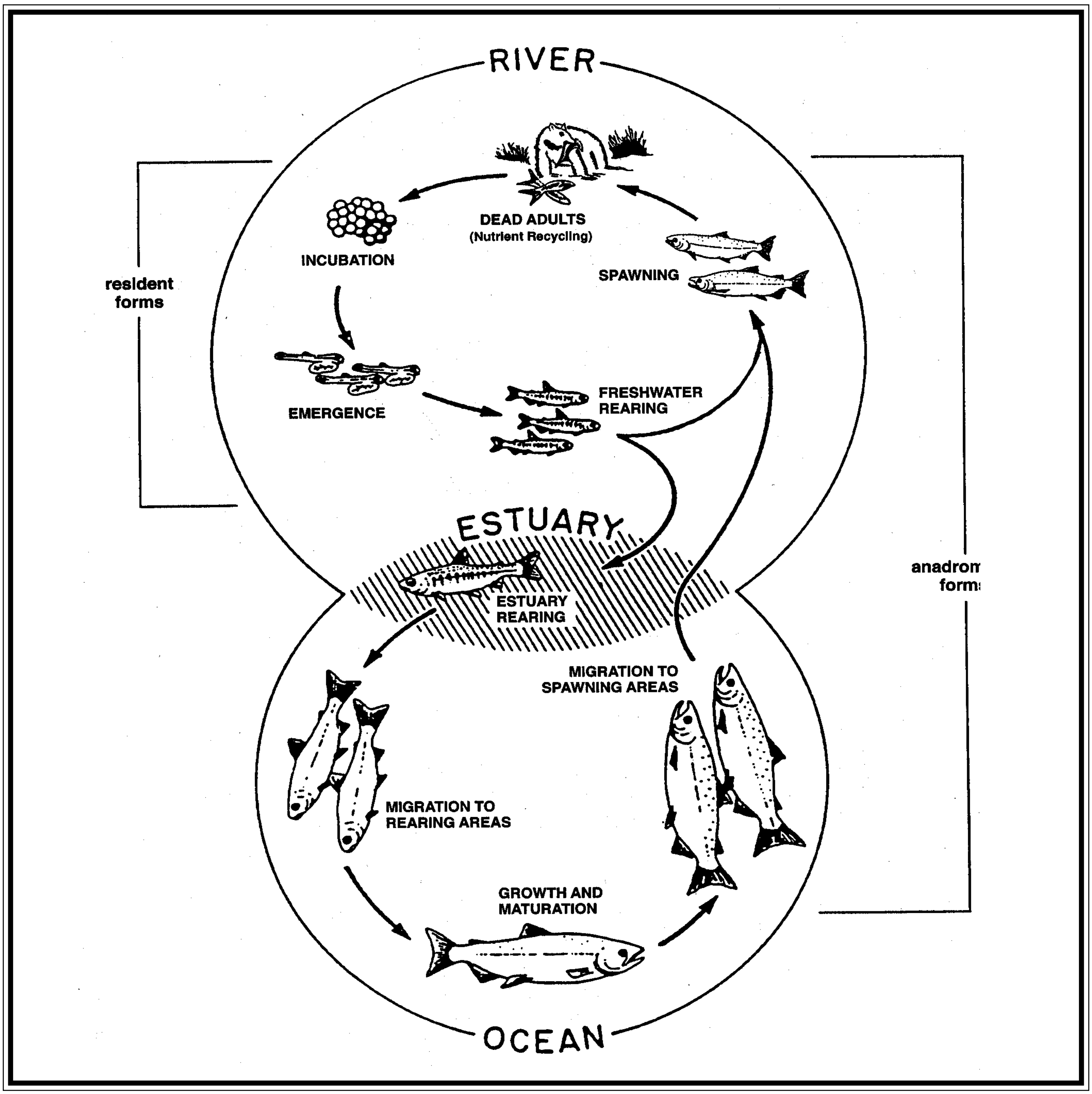


Figure 1. Generalized anadromous and nonanadromous (resident) Pacific salmon life histories, showing freshwater, estuary, and ocean components (the original diagram was from Nicolas and Hankin [372] and later modified by Spence et al. [485]).

Salmon evolved in habitats that are typically characterized by accessible cool, clean water with abundant woody debris or other forms of cover, relatively clean spawning gravels, food, and a balanced population of predators. In the temperate ecosystem of the Pacific Northwest, the freshwater environment is less productive than the ocean environment, particularly estuaries and coastal upwelling zones [179], therefore Pacific salmon evolved an ocean feeding phase in their life history [179]. A typical anadromous salmon life history has five main stages: (1) spawning and egg incubation, (2) freshwater rearing, (3) seaward migration, (4) ocean rearing, and (5) return migration to freshwater to spawn and the deposition of marine derived nutrients into the freshwater ecosystem (Figure 1). Each species has slightly different temporal varieties of the anadromous life history (Figure 2). Simply put, life history means: "...what the salmon do, where they do it, when they do it, and how they do it" [275].

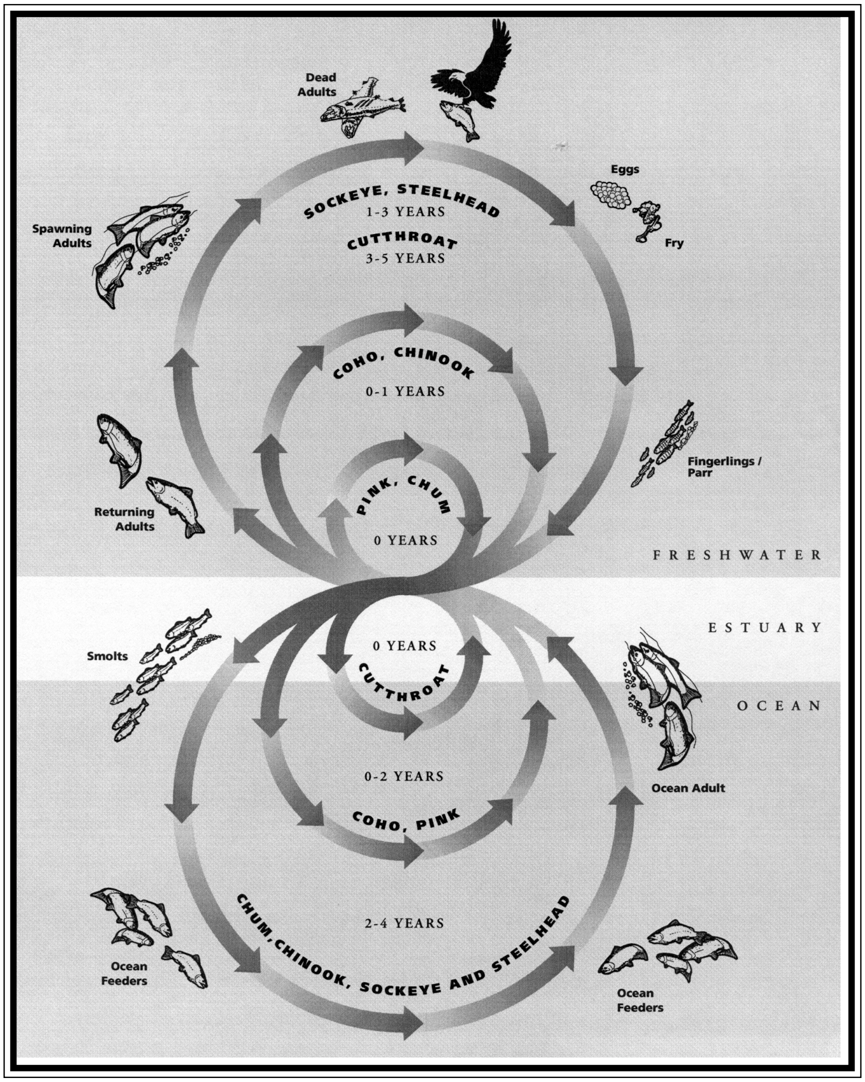
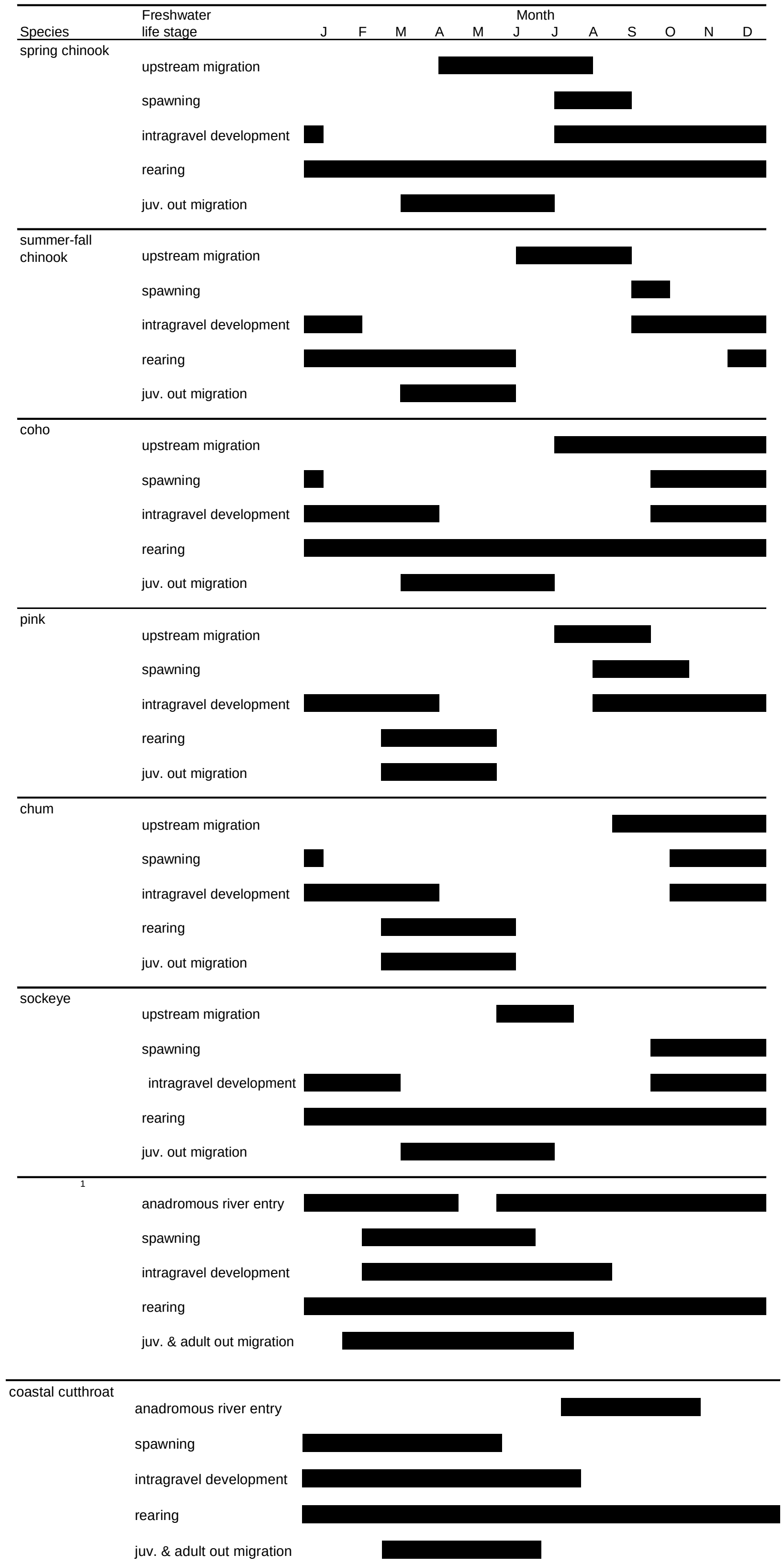


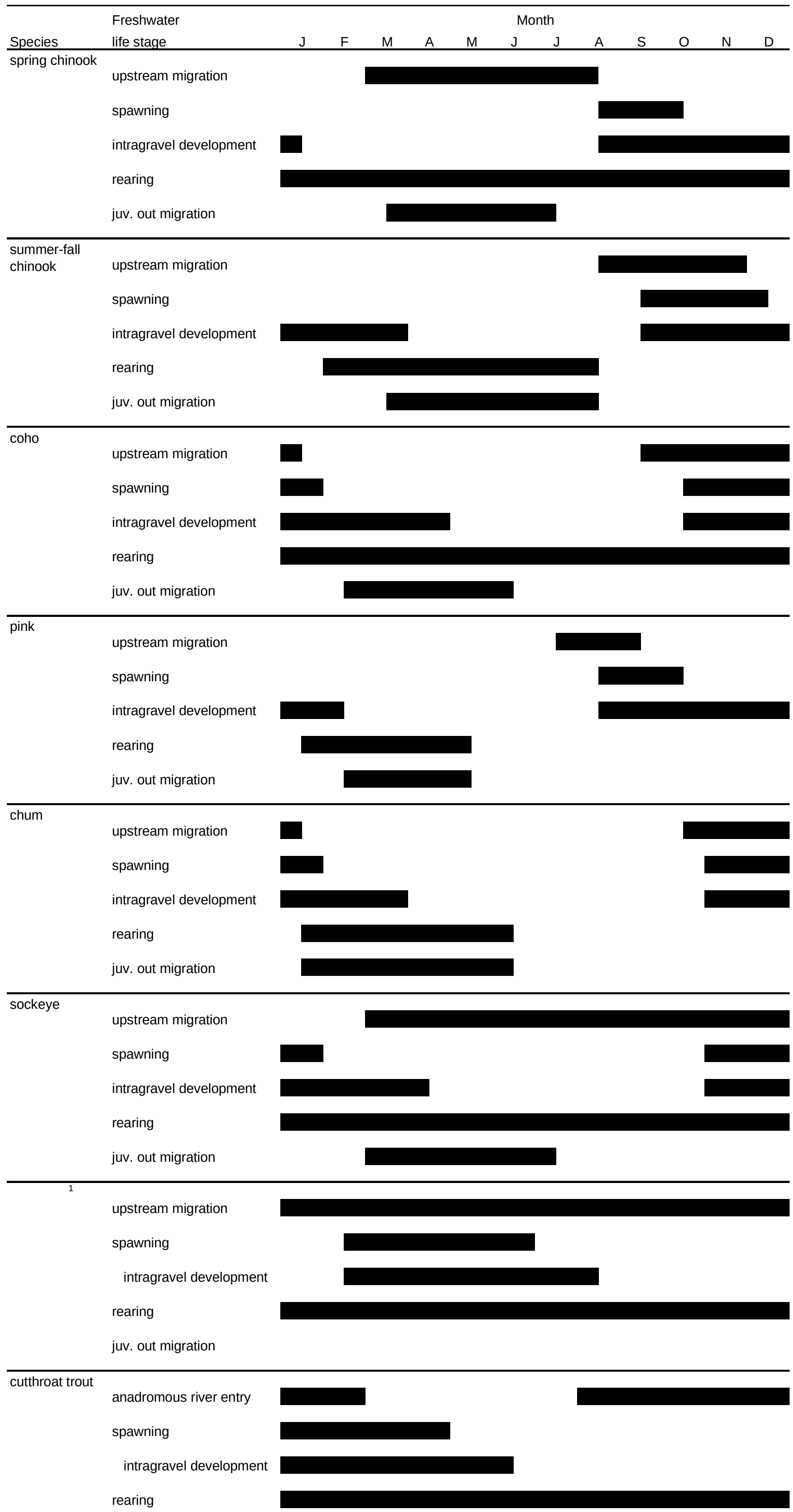
Figure 2. Temporal phases of the anadromous Pacific salmon life history; while in freshwater, estuary, and ocean environments.

The various stages of development may have many different timings, depending on species and location, as typified for Puget Sound (Skagit-Samish Basins) in Figures 3-A, coastal Washington (Queets-Quinault Basins) in Figure 3-B, and coastal Oregon in Figure 3-C. The nonanadromous (resident) life history is typified by spawning and rearing in freshwater without going to sea.



[1] Combines winter and summer races.

Figure 3A. Timing of salmon freshwater life phases in the Skagit-Samish Basins WRIA 03-04 [118, 556, 542, 541].



[1] Combines winter and summer races.

Figure 3B. Timing of salmon freshwater life phases in the Queets-Quinault Basin WRIA 21 [162, 402, 542, 541].

Figure 3C. Timing of salmon freshwater life phases in drainages of the Oregon Coast [79, 234, 356, 372, 505, 549].

The chum, pink, sockeye, chinook, and coho salmon all die after spawning just once, a life history strategy known as *semelparity* [322]. This life strategy has evolved because of the need to have a greater portion of the energy obtained from ocean feeding devoted to gamete production and juvenile survival. Consequently, survival after spawning no longer offered an advantage to these species [322]. Conversely, the death of the spawning run offered a substantial survival advantage to the overall population. By enriching the environment of the juveniles their growth and survival rates could be increased. The *iteroparous*, repeat spawning strategy, typical of the rainbow and cutthroat, probably occurred in the headwater reaches of larger rivers, where nonanadromous populations could be maintained year round. These fish generally were smaller in size, less fecund, and had sparser distribution and lower abundance than the anadromous forms. However, by retaining iteroparity, calamitous losses of young due to floods or drought, could be compensated for in subsequent breeding seasons [322].

Chum, pink, sockeye, chinook, and coho salmon all spawn sometime between August and February, at a time when stream flows are increasing and water temperatures are declining. Rainbow and cutthroat spawn between January and June, when stream flows are decreasing and water temperatures are increasing. For successful development of eggs to occur, the gravel should be relatively stable and clean of fine

Plate #9. Chum salmon spawning in Kennedy Creek, Washington. (Photo by: Jeff Cederholm)

sediments. Pacific salmon are able to clean gravels by purging them of fine sand and silt particles during redd (spawning nest) excavation; but subsequent sediment transport processes and bedload flux can return this environment to the pre-spawning condition [414, 401a]. After approximately 2-4 months of incubation, salmon fry swim up through the gravel and emerge into the stream. Actual emergence time will depend on species and race of fish, for example chum and chinook emerge in late winter-early spring, while coho emerge in middle-late spring, and rainbow and cutthroat emerge in late spring to mid summer. Emerging fry can vary widely in size at emergence, ranging from 20+ mm nonanadromous cutthroat to 35-40 mm chinook. Upon emergence, fry actively feed on a variety of aquatic insects, and for those that freshwater rear for extended periods of time (particularly coho), the proportion of terrestrial food items in the diet may increase to over 30% [338]. Larger-sized juvenile salmon such as older aged rainbow and cutthroat prey on a mixed diet of aquatic and terrestrial macroinvertebrates, and may supplement their diet with occasional salmon eggs or fry [498, 521]. Sockeye fry are known to feed on cladocerens, copepods, and gammarid amphipods in lakes [337].

After a summer of rearing in fresh water, juvenile coho average approximately 50 to 90 mm in length, and may weigh 2 to 5 g each [128, 87]. Summer low-flow is a crucial time in the life of juvenile salmon having extended freshwater rearing. During this period the volume of aquatic habitat shrinks to a minimum, which can intensify inter- and intra-specific competition [9]. Declining streamflow conditions also may cause some fish (i.e., chinook, coho) to emigrate to estuaries [196, 522], where they continue to rear. Where species overlap in fresh water, a number of temporal and behavioral differences facilitate coexistence. For example, age-0 coho (juveniles that have not gone through a winter in fresh water) prefer slow deep habitats called pools, while steelhead age-0 prefer fast-water habitats called riffles, and therefore, are able to coexist in fresh water by partitioning the available food and space resources [96]. On the infertile coast, chinook fry fill a temporal niche in spring prior to steelhead emergence, and thus coexist in a similar habitat until they often migrate to sea after 90 days of rearing in freshwater [282]. Thus, the ratio of fast-water to slow-water habitats and their temporal utilization in a particular stream reach, during spring and summer, can influence the relative proportions of species and age classes of a salmon community.

Upon the first rains and high waters of fall, coastal species (juvenile coho, steelhead, and cutthroat) make a directed migration to seasonally alternate rearing habitats. Juvenile coho and cutthroat exhibit major immigrations into side-channel swamps [80] and riverine ponds [398, 400, 94, 162], located along river flood plains. Juvenile coho, steelhead, and cutthroat are known to immigrate into small "runoff" tributaries (valley-wall tributaries) of rivers [94, 271]. Presumably these immigrations are to avoid high flows and turbidity of main rivers, as well as to take advantage of good feeding conditions during winter [398, 399]. In contrast, interior (Idaho) juvenile chinook are known to move out of tributaries and into main rivers to over-winter, likely to avoid winter ice conditions in the tributaries [57].

After completing their freshwater stage, juvenile salmon of all anadromous forms undergo a physiological change called smoltification that includes osmoregulatory adjustments which prepare them to enter saltwater. For example, chum and pink salmon are nearly smolts upon emergence from the gravel, going directly to estuaries and the ocean [259, 440]; while chinook [197] and coho [442] may either go directly to sea the first spring or summer of their life, or remain in freshwater for a whole year before smolting. Sockeye may rear in freshwater for one or two years before smolting [77], and steelhead [283] and cutthroat [160, 162] may not smolt for two or three years or more.

Once in the estuary or ocean, most salmon prefer to feed on such prey as amphipods, copepods, euphausiids, squid, herring, sandlance, rockfish, and anchovy [83, 83a, 197]. While in the ocean, most salmon species migrate long distances to feeding grounds along the North Pacific coast [178, 135, 136, 196, 194]. In contrast, some chinook stocks remain as "blackmouth feeders" in Puget Sound and the Strait of Georgia [573], never going to the open ocean; and anadromous cutthroat may only range several kilometers from their natal stream without overwintering in the ocean [395]. Depending on the species, salmon use the ocean as a feeding ground in vastly different ways, some stay close to the North American Continent (i.e., chinook, coho, and cutthroat) and others (i.e., sockeye, chum, pink, and steelhead) forage far out into the north and western Pacific Ocean; but all survivors eventually return marine derived nutrients back to their rivers of origin at adulthood (Figure 4).

During their anadromous life history salmon make important ecological contributions (as prey) to various predators in the Pacific Northwest ecosystem, regardless of whether a particular individual salmon

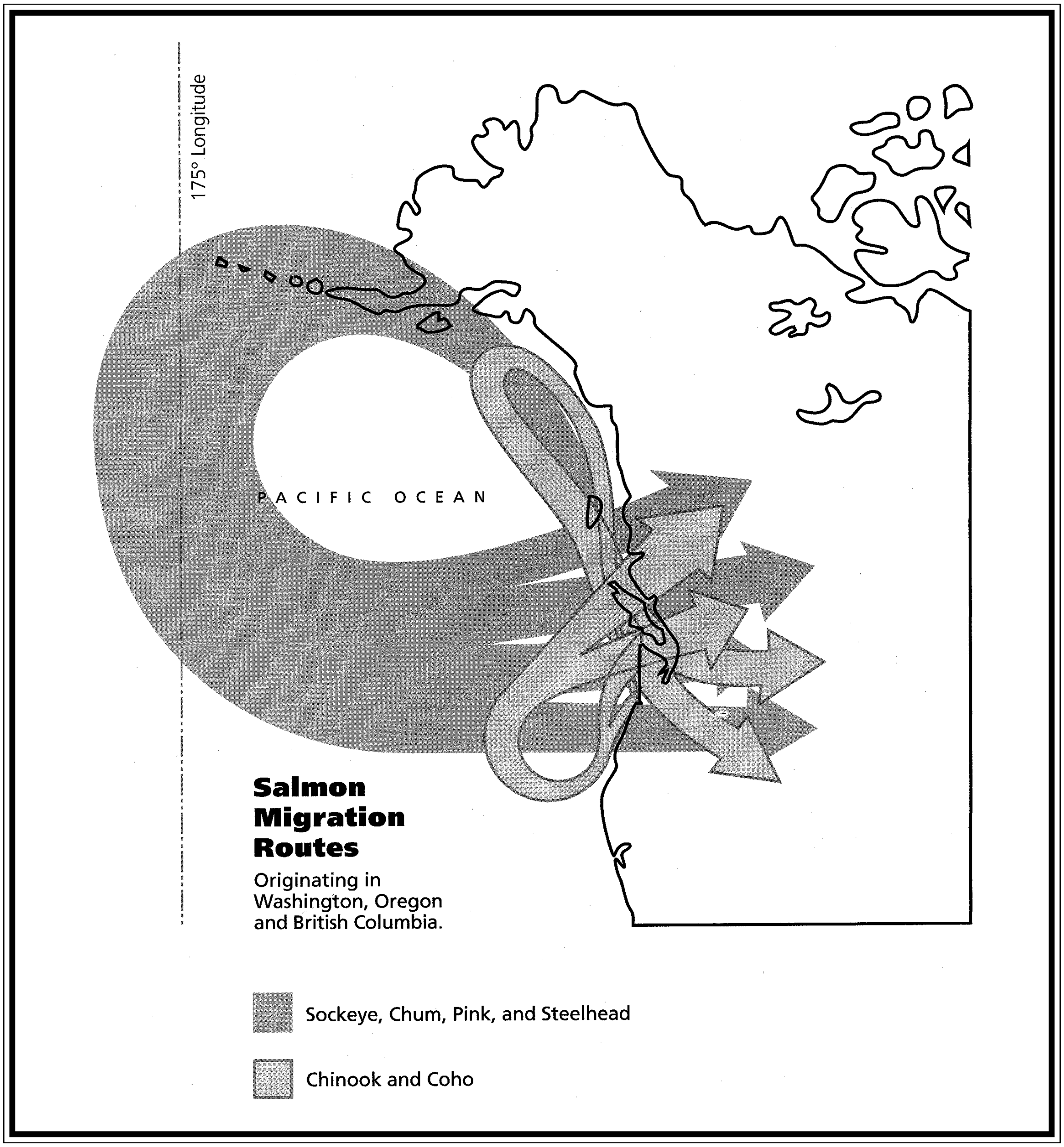


Figure 4. Generalized ocean migration routes and biomass accrual of six species of Pacific salmon originating in Washington, Oregon, and British Columbia.

completes all life history stages or not (Figure 5). It is not uncommon for overall salmon survival rates to average 0.1% from egg to spawning adult.

Chum Salmon (*Oncorhynchus keta*)

Chum, or "dog" salmon spawn in the late summer into winter, depending on location. They deposit their eggs in a redd, and the incubation period can last from 3-5 months, depending on water temperature. There are mainly two races of chum salmon in Washington, the summer chum and the more abundant fall chum [259]. Some chum spawn intertidally, but most spawn in the lower reaches of rivers and streams. Chum salmon prefer medium sized gravel that is free of excessive amounts of sand [259]. The freshwater phase of juvenile chum salmon is virtually over upon fry emergence from the gravel, at which time the fry migrate to protected marine waters and estuaries. Here they rear for several weeks before migrating to the ocean [440]. The length of time spent in the ocean can vary, but generally chum salmon grow to 3 or 4 years of age. Chum in Hood Canal can reach weights of 3.1 to 6.2 kilograms, depending on sex, stock, and year [259] (Table 2).

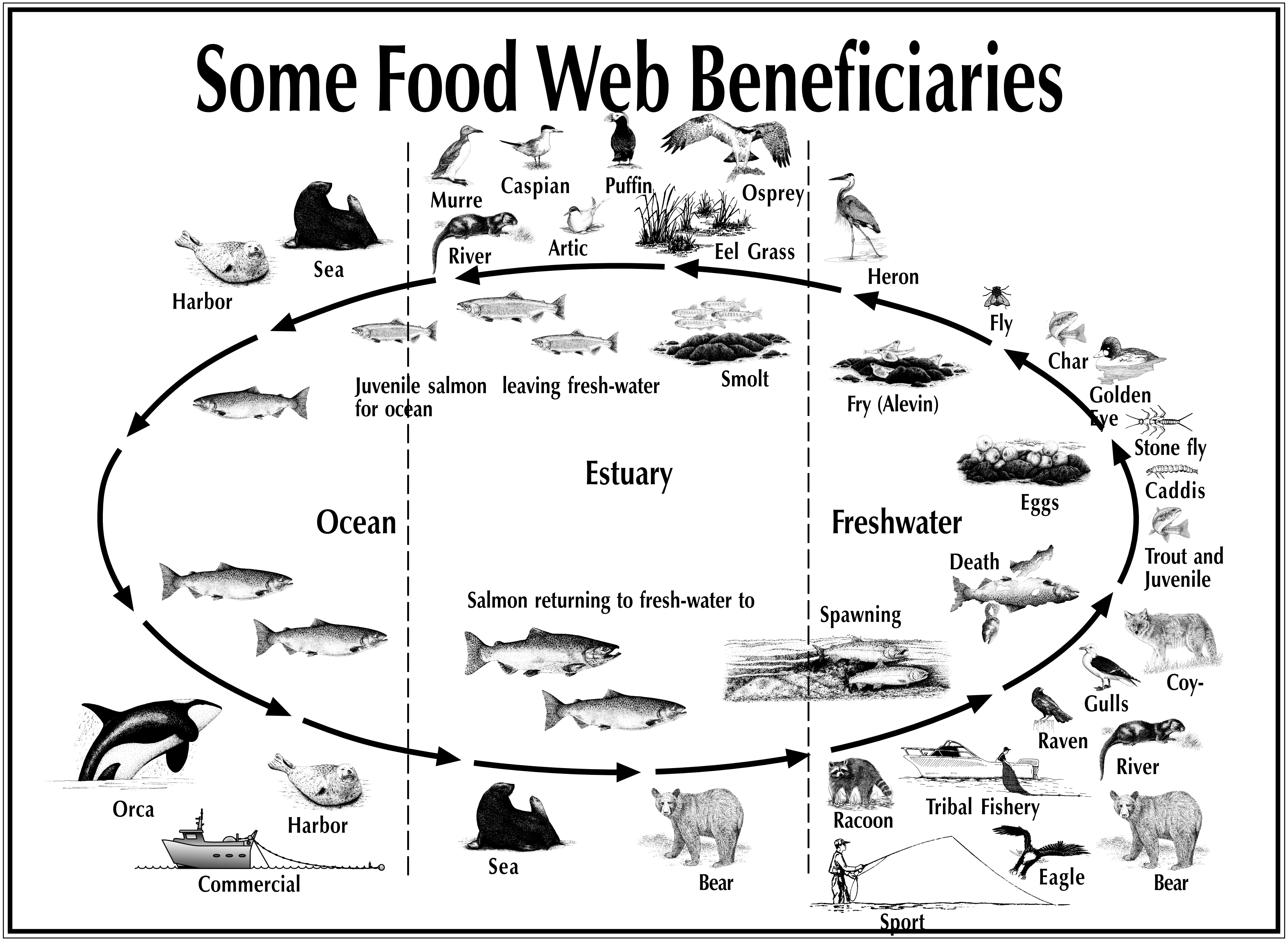


Figure 5. Some food web beneficiaries of Pacific salmon nutrient in freshwater, estuary, and ocean environments.

Pink Salmon (*Oncorhynchus gorbuscha*)
Pink, or "humpy" salmon, like the chum salmon, use freshwater almost exclusively as an incubation environment, preferring to feed in estuaries and saltwater. Like the chum salmon, there are both summer and fall pink salmon, with falls predominating in run size. Pink salmon often spawn in the lower reaches of rivers and streams, and many are known to spawn in the intertidal areas [198]. Spawning is usually complete by fall or early winter. Upon emergence from the gravel, pink salmon fry go directly to the ocean for rearing. Pink salmon are unique in that they have a strict 2 year life span, and in Washington the odd year cycle dominates [573]. Adult pink salmon average about 1.8 kilograms in weight [573] (Table 2).

Sockeye Salmon (*Oncorhynchus nerka*)
Sockeye salmon, also called the "red" salmon, are unique because they generally use rivers that have an accessible lake environment in their drainage [146]. Most sockeye adults enter freshwater in early to mid-summer, hold in a lake, and spawn in fall. Typically sockeye spawn in inlet or outlet tributaries of lakes, while some sockeye spawn in upwelling water along lake shorelines. Sockeye embryos have adapted to the reduced oxygen environments typical of the upwelling areas in lakeshore, stream, and spring areas [77]. Reduced egg size, egg features that enhance oxygen transfer capabilities to the embryo, and a generally longer incubation period than other Pacific salmon, are some of those beneficial adaptations. The length of time spent in freshwater as juveniles varies from 1 to 2 years; while an additional 1 to 3 years is spent in the ocean rearing to adulthood. Most adult sockeye average between 1.5 to 3.6 kilograms in weight [573] (Table 2).

There is a nonanadromous form of sockeye called "kokanee". The kokanee is much smaller in size at adulthood because it spends its entire life feeding in freshwater. Adult kokanee weigh about 0.5 to 1 kilogram.

Chinook Salmon (*Oncorhynchus tshawytscha*)
The chinook, or "king" salmon, is classified into three distinct varieties (spring, summer, fall) based on the season they enter freshwater as adults. They tend to spawn in large rivers and their tributaries, preferring deeper water and larger gravel substrate than the other species. Spawning usually occurs between August and November, depending on the particular variety. After fry emergence in winter and early spring, some "ocean-type" chinook swim downstream to the ocean within several weeks, while others "stream-type" spend up to a year feeding in freshwater before they migrate to sea [197]. Migrant chinook exhibit major use of estuaries, particularly large marsh habitat (i.e., Skagit River, Fraser River) where they feed on amphipods. During their winter in freshwater, juvenile chinook have been found buried within gravel spaces, presumably to escape high stream flow conditions [56, 57]. The length of time spent at sea varies, but most chinook salmon return to spawn at age 3 to 5 years. Chinook have been known to reach weights of over 45 kilograms, however, most range between 5 and 10 kilograms [573] (Table 2).

Coho Salmon (*Oncorhynchus kisutch*)
The ubiquitous coho salmon, also called the "silver" salmon, occur in almost every accessible coastal stream. Coho spawn in October through December, depending on the particular stock [442]. Fry emerge from the gravel in April and May [510], and spend a summer feeding in pools or slow moving river side channels [80]. In the fall, when stream flows increase, coho juveniles move downstream from their summer rearing habitats and immigrate into small flood plain tributaries and riverine ponds [80,94,401]. Most smolting coho migrate to sea between the months of April and June, at age-1, but in cooler waters may remain a second year in freshwater. Coho spend about a year feeding in the ocean, then return to their natal stream to spawn at age-3 [439]. Coho average between 3.6 to 5.4 kilograms as adults [573] (Table 2).

Rainbow Trout (*Oncorhynchus mykiss*)
Rainbow trout are found in most coastal and interior rivers, favoring cold-fast flowing environments [498]. There are two main subgroups of rainbow, the anadromous and nonanadromous forms. The anadromous rainbow are called steelhead. There are two main varieties of steelhead , the so called "winter-runs" and "summer-runs". Winter-run steelhead tend to predominate in coastal and Puget Sound rivers; while summer-run dominate in the interior Columbia and Snake River drainage. Nonanadromous forms of rainbow tend to exist in the headwaters of many rivers where there are steelhead. During freshwater rearing, juvenile steelhead are often found in riffle environments, where they are able to minimize competition with juvenile coho [9], but parr are also common in pools (Pat Slaney, personal communication). In the fall and early winter, juvenile steelhead redistribute and take up overwinter residence in small runoff tributaries [94,560], avoiding

riverine ponds where juvenile coho reside [94]. Juveniles are also known to bury themselves in the substrate during winter, presumably for protection against high flow conditions [56]. Generally, juvenile steelhead spend two years in freshwater before smolting, however, some spend 1 year or 3 years. They spend an additional 1 to 4 years in the ocean, and return to spawn at age 2 to 5. Steelhead may reach weights of 13 kilograms, but most weight in the 3 to 6 kilogram class (Table 2).

Coastal Cutthroat Trout *(Oncorhynchus clarki clarki)*

Coastal cutthroat trout, also called "harvest trout", are found in most Washington and Oregon coastal streams [521]. Two main sub-groups of coastal cutthroat have been found living in tributaries of coastal rivers, the anadromous and nonanadromous forms. Anadromous (sea-run) cutthroat enter freshwater from the ocean in late summer and fall to either feed or spawn [238]. The nonanadromous form is characterized by both the non-migratory (fluvial) and within river migratory (potamodromous) types [162]. Spawning occurs in late winter through spring. After incubation fry emerge during late spring and early summer and take up residence in shallow riffles and pools in small headwater tributaries, usually upstream of all other species of salmon. This spatial segregation allows younger individuals to avoid direct competition with other salmon juveniles [166]. In preparation for winter, juvenile cutthroat are known to *move downstream* and immigrate into flood plain tributaries to over-winter, similar to the movements of juvenile coho and steelhead [94,162]. Anadromous cutthroat spend 2 to 5 years in fresh water before going to sea [160]; however, they seldom over-winter in saltwater [395]. A large sea-run cutthroat trout would be 24 inches long (Table 2).

Table 2. Key sources of life history information for the 7 salmon species of Washington and Oregon.

Species	Reference
chum	Wydoski and Whitney [573], Salo [440], Koski [259], Bjornn and Reiser [56], Everest et al. [140].
pink	Wydoski and Whitney [573], Heard [198], Bjornn and Reiser [56], Everest et al. [140].
sockeye	Wydoski and Whitney [573], Burgner [77], Foerster [146], Bjornn and Reiser [56], Everest et al. [140].
chinook	Wydoski and Whitney [573], Healey [197], Bjornn and Reiser [56], Bjornn [57], Everest et al. [140].
coho	Wydoski and Whitney [573], Sandercock [442], Tagart [510], Bustard and Narver [80], Salo and Bayliff [439], Cederholm and Scarlett [94], Peterson and Reid [401], Bjornn and Reiser [56], Everest et al. [140].
steelhead	Wydoski and Whitney [573], Stolz and Schnell [498], Bjornn and Reiser [56], Allee [9], Winter [560], Cederholm and Scarlett [94], Everest et al. [140].
cutthroat	Wydoski and Whitney [573], Glova [166], Trotter [521], Johnston [238], Garrett [162], Fuss [160], Pearcy [395], Cederholm and Scarlett [94], Everest et al. [140], Hall et al. [181].

FRESHWATER AND TERRESTRIAL HABITAT RELATIONSHIPS OF SALMON

Freshwater Habitat

Freshwater habitat of salmon includes all the physical, chemical and biological elements within the aquatic environment. Geology, climate, topography, disturbance history, nutrients from returning salmon, and characteristics of the riparian vegetation typically govern the characteristics and the distribution of habitat types in a watershed. Components of freshwater habitat include:

Physical Characteristics - channel width and depth, substrate composition, pool and riffle frequency, pool types, channel roughness.
Water Quality and Quantity **-** temperature, dissolved oxygen, dissolved nutrients, dissolved and particulate organic matter, hydrography.
Cover factors **-** interstitial spaces (space between gravels), undercut banks, woody debris, water surface disturbance.
Biological Factors **-** food availability, salmon carcass nutrient inputs, competition, predation, disease, parasites, and functioning riparian conditions.

Climate and regional geology determine habitat conditions at large spatial scales. The type of bedrock, the glacial history, and precipitation patterns contribute to landscape and channel morphology [38]. In Washington, the South Fork of the Stillaguamish River (like many Puget Sound rivers) was heavily glaciated, creating a landscape of steep, highly dissected hill slopes in the headwaters, and terraces formed by glacial outwash in the valley bottoms [38]. The land form dictates the channel gradient, from gentle hill slope morphology on terraces, to steep and precipitous conditions in the headwaters, and plays a large role in shaping the salmon habitat characteristics in the channels [33]. Streams draining outwash terraces, which have little topographic relief, typically exhibit gradients less than 4% and contain abundant pool habitat. Stream channels on these terraces support many of the anadromous fish populations in the watershed [33].

Plate #10. Low gradient stream showing large woody debris formed habitat in Monroe Creek, Washington. (Photo by: Jeff Cederholm).

This change of channel conditions from the headwaters downstream is typical of many watersheds in the

Pacific Northwest and correlates well with shifts in the fish communities . Montgomery and Buffington [332] described various channel forms and have developed a classification system based on channel size, gradient, and the presence of roughness elements. The geomorphic classification of stream channels allows one to better understand the distribution of the various salmon species within a watershed. For example, the anadromous forms are usually located in the downstream low gradient reaches, where they have unimpeded upstream and downstream passage; while the resident nonanadromous forms are located in the middle to upper steep headwater areas. The distribution of various species of salmon in a drainage has been discussed by Reeves et al. [417].

Plate #11. Hoh River on the western Olympic Peninsula. (Photo by: Jeff Cederholm).

The abundance of fish in a stream is greatly affected by the stream's capacity to produce food. Many of the factors influencing stream productivity change predictably with changes in stream size, a pattern termed the *river continuum* [529]. Productivity is influenced by nutrient availability, input of organic matter from external sources, and the capacity for the channel to store and process organic matter, and light.

Differences in these factors can be very large and lead to a high degree of variability in production of fish, including salmon and trout populations [223]. Some of the highest freshwater production values have been reported for trout in New Zealand spring streams, 54.7 g/m2/y [10]; however, production values from the Pacific Northwest are generally low when compared with other regions of the world, often below 1.0 $g/m^2/y$ and very rarely over 5.0 $g/m^2/y$ [55].

Riparian Habitat

Many of the functional and structural attributes of stream habitat are created and maintained through interaction with riparian vegetation. Riparian areas constitute the interface between aquatic and terrestrial ecosystems [506, 171], performing a number of vital functions that affect the quality of salmon habitats as well as providing habitat for a large variety of terrestrial plants and animals. Riparian areas influence streams and consequently salmon habitat in a variety of ways [485], including:

> *<u>Shade -</u>* which dampens seasonal and diel fluctuations in stream temperature and controls primary and secondary production.
> *<u>Streambank stabilization -</u>* provides erosion resistant roots that bind soil particles together, thus facilitating bank building during high flow events by slowing the stream velocities.
> *<u>Sediment control -</u>* regulates sediment flow from upland areas by acting as a filter, or storing sediments in the primary flood plain.
> *<u>Litter Input-</u>* contributes a significant amount of organic matter to streams, which acts as an important food resource for aquatic communities.
> *<u>Large woody debris (LWD) -</u>* provides important structure to the stream channel for energy dissipation, fish habitat, and salmon carcass retention.
> *<u>Nutrient input -</u>* riparian zones mediate the flow of nutrients to the stream and are, therefore, important regulators of stream production. Some riparian species such as red alder (*Alnus rubra*) also fix atmospheric nitrogen therefore augmenting N availability to the ecosystem.
> *<u>Microclimate -</u>* streamside soils and vegetation can have a significant effect on moderating the climate within riparian zones.

Streamside vegetation moderates water temperature, and this relationship is influenced by elevation, air temperature, stream width, water depth, and aspect [41]. Removal of riparian vegetation has been associated with increased maximum water temperatures, and diurnal fluctuations in water temperature during summer; and decreased winter water temperatures [41]. Small, low-elevation streams are the most susceptible to summer water temperature increases caused by canopy removal [504]. The biological consequences of elevated water temperature on aquatic communities are complex. There is little information indicating direct mortality of fishes as a result of temperature changes related to riparian canopy removal [41]; however, reductions in growth rate [51, 572], changes in life history [215], changes in competitive interactions between species [418], reductions in fecundity of adults [40], and an increased susceptibility to disease [386, 363], have all been documented. Some species of amphibians and aquatic macroinvertebrates also are thermally intolerant and elevated water temperatures may have detrimental impacts on their populations [327, 137, 78].

Riparian vegetation increases streambank stability and resistance to erosion. Roots from woody and herbaceous vegetation bind soil particles together, helping to maintain bank integrity during erosive high-streamflow events [506, 485]. Riparian vegetation also facilitates bank-building during high flow events by slowing stream velocities, which in turn helps to filter sediments and debris from suspension. This combing action helps to stabilize and rebuild streambanks, allowing the existing channel to narrow and deepen, and increases the effectiveness of riparian vegetation in providing bank stability and shade [132]. During over-bank flows, water is slowed and fine silts are deposited in the flood plain, increasing future productivity of the riparian zone [485].

Forested riparian areas generate much of the organic matter that provides the energy source for the trophic systems of small streams. In one study of forested headwater channels in Oregon, Sedell et al. [452] determined that over 90% of the in-channel organic matter was provided from the surrounding terrestrial environment. A 10-m wide stream in western Washington received over 75% of its annual organic matter supply from terrestrial sources [46]. Even though this source of organic matter decreases relative to autochthonous organic matter in larger channels, it remains vital to stream productivity.

Large woody debris has been shown to be a critical structural component in Pacific Northwest streams, forming pools, waterfalls, and overhead cover; and it also regulates the transport of sediment, gravel and organic matter, for fish and other aquatic biota [50, 49]. In forested watersheds LWD provides the most common obstruction, often forming pools in various types of fluvial channels [332]. Without this material, pool abundance and size is decreased [45], reducing habitat complexity and potentially reducing the diversity of the fish community. In addition to numerous habitat and morphological functions [50], wood (organic debris) helps retain salmon carcasses in streams for biological activity [90]. The capacity of many small streams to retain carcasses has probably been reduced by human activities, and this could have serious impacts on the food chain of fishes, and on the available food supply of many carnivorous wildlife species [91].

Riparian areas play a key role in determining the concentration of nutrients in stream water [42]. The presence of even a narrow riparian buffer can profoundly influence stream water chemistry. Uptake and storage of various elements carried by groundwater can be considerable, even where input rates have been substantially altered as a result of upslope land uses [284]. Riparian vegetation composition can influence nitrogen input to streams. Early successional vegetation in riparian areas in the Pacific Northwest is often dominated by red alder, a nitrogen (N) fixing species. As a result, the N content of litter beneath these riparian stands is 1.5 to 3-fold higher than sites where conifer species are the dominant component of the over story [128a]. The result is higher N levels in the riparian soils [58] and increased delivery of N to the stream channel. Higher N levels in stream water may elevate primary production and decomposition (heterotrophy) in the channel and increase food availability for the invertebrate community. Increased invertebrate production may elevate food availability for stream-dwelling fishes, amphibians, and other insect feeders such as bats and flycatchers.

The riparian area may act as either a source or sink of organic matter and sediment during flood flows. The manner in which the stream and riparian area interact at these times depends upon the morphology and vegetation of the riparian zone and the intensity of the discharge event [34]. The structure and abundance of riparian vegetation plays a key role in moderating the movement of materials between the riparian area and the stream [361]. Vegetation in the riparian zone has been shown to be the single most important structural element for the retention of fluvially transported organic matter during high flow events [484]. Similarly, riparian vegetation promotes the storage of sediment [216], that may provide germination sites for some species of riparian plants [370]. The variations in retentive capacity of different riparian areas for organic matter leads to large differences in the organic content of riparian soils, ranging from nearly all inorganic material in some locations to very high concentrations of organic matter in stream-adjacent swamps and wetlands [71]. This variation in substrate further contributes to riparian vegetation heterogeneity [2].

The area, in which water exchange between the channel and the underlying riparian soils occurs is termed the *hyporheic zone* [491]. The extent of the hyporheic zone varies as a function of site topography and soil characteristics. In riparian areas of low relief and porous soils, the hyporheic zone may extend as far as 3 km from the edge of the channel [491]. The riparian vegetation has an influence on the amount of water stored in the hyporheic zones. Hicks et al. [207] found that August stream flows following logging of a small western

Cascade Mountain watershed, including the removal of riparian vegetation, increased for 8 years as a result of reduced transpiration. Subsequently, as early successional vegetation occupied the riparian area, summer stream flows decreased to below pre-harvest levels due to high transpiration associated with this vegetation type. Riparian vegetation, through its influence on riparian soil characteristics and water movement, also can impact chemical transformations within the hyporheic zone [520]. Along low-gradient, unconstrained stream reaches, vegetation-hyporheic interactions may occur over a broad area. In areas of moderate to high topographic relief the zone of direct interaction between vegetation and the hyporheic zone will be reduced.

The attractiveness of riparian areas to wildlife likely reflects three main attributes: the presence of water, local microclimate condition, and more diverse plant assemblages found in riparian areas compared to uplands. Wildlife also congregate seasonally in riparian areas where salmon spawn, to take advantage of an abundant food supply of carcass flesh [91]. The high value of riparian habitats to wildlife has been recognized by naturalists [380], and considered a bridge between upland habitats and the aquatic environment. The combination of shape, moisture, deposition soils, and disturbance regime unique to riparian areas contributes to their exceptional productivity in terms of plant growth, plant diversity, and structural complexity of the vegetation [237, 329, 270]. Wildlife dependency and diversity peak at this terrestrial/aquatic boundary. Brown [69] reports that 359 of 414 (87%) species of wildlife in western Washington and western Oregon use riparian areas and wetlands during some season or part of their life cycle. In their detailed examination of wildlife and habitats for all of Washington and Oregon, Johnson and O'Neil [236] reported that 393 of 456 (86%) of the common terrestrial and freshwater wildlife species have seasonal use of riparian areas, wetlands, and streams. Of these 393 species, 110 were found to be *closely associated* (e.g., obligates) with eastside and westside riparian habitat types.

The close association may very well have evolved from the direct or indirect exploitation of the rich vegetative habitat provided by riparian areas [255]. Quantitative studies conducted during the past several decades have supported observations and have identified biological and physical attributes of riparian habitats which enhance their value to wildlife. Brinson et al. [64] and Oakley et al. [381 cited in 380] summarize these important biological and physical features of riparian areas:

- presence of surface water.
- increased humidity, high rates of transpiration, and greater air movement.
- complexity of biological and physical habitats.
- maximum edge effects with adjacent upland forests which is beneficial for some species.
- food supply.
- thermal cover.

According to O'Connell et al. [380] stream type has a direct influence on the riparian habitat and its associated wildlife communities. In the smaller headwater streams the impacts of the upstream riparian vegetation on the streams is greater than downstream where flow volume increases, flooding is more widespread, and the impact of riparian vegetation on the stream is less. Brinson et al. [64] suggest that middle order perennial streams and associated riparian areas have the greatest wildlife use. Periodic flooding can enhance the availability of food for wildlife by creating new feeding areas [64]. Flooding can also make riparian habitat unsuitable for other species. Species abundance of riparian mammal communities has been related to the timing of recent hydrologic events; impoverished mammal populations have been attributed to recent flooding whereas more abundant populations have been observed in areas not subject to recent flooding [64].

Habitat Forming Processes

Disturbance plays a major role in maintaining community diversity and productivity in many ecosystems [105, 420], and is a key factor in creating and maintaining diverse stream habitat in the Pacific Northwest [38a, 54]. These disturbances range in severity from minor events, such as seasonal changes in flow, to less frequent high intensity events such as wildfire, debris torrents, and major floods. Riparian and channel conditions evolve as impacted areas recover from disturbance [211]. The result is a diverse set of riparian community types and stream habitat conditions that vary over both time and space [2].

Disturbance contributes to both diversity of aquatic fauna and productivity of these communities when considered at a watershed level [173]. Aquatic communities associated with early-successional riparian areas typically exhibit low diversity, but high productivity for certain species. Removal of the channel shading canopy brings about dramatic increases in light and algal productivity; however, input of terrestrial litter decreases [172, 46]. Invertebrates that feed on algal material (grazers) typically dominate communities at recently disturbed sites, [137]. These invertebrates form a major component of the diet of some salmon and trout [338] and can contribute to increased fish productivity following disturbance [352, 52, 46]. The increased productivity is typically observed during summer, and often does not extend into winter months when the availability of shelter from high flows for juvenile salmon becomes important [94, 401, 162].

After forest canopy closure, primary productivity in streams decreases. The type of litter delivered to these systems and the physical characteristics of the channel differ from those at sites bordered by mature vegetation. Hardwood trees, especially red alder, often dominate the canopy at these sites. Litter from red alder trees decomposes much more rapidly than conifer litter, in part due to the higher N content [451]. The high N content of the litter improves its nutritional value for shredding macroinvertebrates but the high rate of decomposition causes it to be scarce at some times of the year.

Alder stands begin to die-out and provide LWD to channels after about 60 years [175]. Shade tolerant conifers, like western red cedar (*Thuja plicata*) and western hemlock (*Tsuga heterophylla*) colonize the site and begin to provide needles and other litter to the channel. Some stands of alder can persist and will repeat themselves several times (Slaney, personal communication). Woody debris amounts and average piece size increase for 100 or more years following conifer occupation of a site [506, 44]. The morphology of the channel and the routing of sediment and organic matter evolve slowly as the riparian community changes, ultimately creating channels which are highly complex structurally and support a macroinvertebrate community dominated by shredders [11].

Forest practices and other land uses have accelerated the rate of occurrence of some types of disturbance. The acceleration in disturbance has led to the establishment of early successional communities in the majority of riparian areas on commercial forest land in the Pacific Northwest [60, 86, 154]. Practices, such as splash damming of rivers to float logs to market [550], and removing all trees to the channel's edge [43] modify the riparian successional process. Timber harvest or roads constructed on unstable slopes or road drainage systems that were improperly maintained, dramatically increase the incidence of landslides [421, 93, 456]. Many hillslope failures enter stream channels and may move considerable distances downstream, removing streamline vegetation and soil. On the positive side, however, localized landslides also can input massive amounts of spawnable sized gravels and LWD into stream channels, where they may benefit salmon populations [456]. These disturbance events have affected a large proportion of the riparian areas bordering streams in the region over the last century, and have played a key role in determining channel form and habitat conditions [507].

From a study of fire history in Mt. Rainier National Park, Hemstrom and Franklin [201] reported that alluvial terraces and valley bottoms were often forested with old stands and that every major river valley contained a stream-side old-growth corridor. These observations support an inference that the moist environment of riparian areas inhibits fire and reduces the fire return interval for riparian forests. The moister environment may also advance the regeneration of more structurally complex forest following wildfire. Fires that burn across riparian areas may be less intense, and less intense fires would kill fewer trees and consume less coarse woody debris, both snags and logs. The persistence of live trees in riparian forests may also provide a local seed source that facilitates a more rapid development of a multi-layered, conifer-dominated forest [405].

Beaver

Beavers have long co-existed with salmon in the Pacific Northwest, and have had a important ecological relationship with salmon populations. The beaver created and maintained a series of beneficial aquatic conditions in many headwater streams, wetland, and riparian systems, which serves as juvenile salmon rearing habitat. Beavers have multiple effects on water bodies and riparian ecosystems that include altering hydrology, channel morphology, biochemical pathways, and stream productivity [385]. Beaver ponds were of special importance in more arid regions, but also had important roles in coastal systems [365]. Beavers were once extremely abundant in the Pacific Northwest, but as far back as 1778, trapping expeditions into western North America began depleting their numbers. Between 1834 to 1837, pelts from 405,472 beavers from the area that would become southwest Washington and Oregon were shipped to Europe. It is difficult to imagine the amount of influence beavers have had on the landscapes, most Pacific Northwest streams have been void of beaver activity for many decades before ecologists had the opportunity to study them.

Past excessive trapping, and subsequent unregulated land- and water-use activities, significantly reduced abundance of beaver and beaver ponds. Even ponds of the surviving beavers were actively removed. Additionally, excessive livestock grazing in riparian areas has degraded habitat conditions for beaver [385]. Severe declines of beaver in Washington and Oregon have fundamentally altered important natural aquatic ecosystem processes such as nutrient cycling, flood plain development, and stream hydrology.

Beaver dams can obstruct channels and redirect channel flow and the flooding of streambanks and side channels. By ponding water, beaver dams create enhanced rearing and over-wintering habitat that protect juvenile salmon during high flow conditions [365]. Studies in Oregon coastal streams have suggested that where the amount of spawning is adequate, the winter survival of juvenile coho, which can be swept downstream in high winter flows, is limited by the presence of adequate slow-water habitat [374]. Beaver dams are often found associated with riverine ponds called “wall-base channels” [401] along main river flood plains, and these habitats are used heavily by juvenile coho salmon [400, 94] and cutthroat trout [94, 162] during the winter. Though their dams can occasionally block upstream migration of adult and juvenile salmon, studies of trout movement indicate that fish can pass over beaver dams during all seasons [385]. Beaver dams may temporarily keep salmon adults in the lower parts of spawning streams where flows are greater and pools are deeper, then, when dam breaching flows occur, free passage to upstream areas is provided.

Beaver foraging can cause a loss of woody riparian vegetation and an increase of fine sediments, but it also increases the input of large woody debris to streams and beaver droppings may enrich pond productivity. Bank dens and channels can increase erosion potential, but because ponds fill with sediment to become wetlands over time, this helps to retard upstream erosion and retain sediments that otherwise could adversely alter downstream areas [485]. In a Wyoming study of an area that had 10.5 beaver dams per km, each dam was found to retain 5,350 m^3 of sediment. In another Wyoming study, sediment loads were reduced by 90% after flowing 8 km through an area with well developed riparian habitat and beaver dams.

Beaver ponds provide a sink for nutrients from tributary streams and create conditions that promote anaerobic decomposition and de-nitrification. These processes can cause nutrient enrichment and increased primary and secondary production downstream from the pond and increasing nutrient retention time and enhanced invertebrate production in the pond [365]. These factors help increase salmon growth and survival, and also helps improve water quality. Beaver ponds increase the surface to volume ratio of the impounded area, which can result in increased summer temperatures [485]. Beaver ponds also can cause increased storage of water in the banks and flood plains, and this increases the water table, enhances summer flows, adds cold water during summer, and causes more even stream flows throughout the year. During winter, beaver ponds in cold environments prevent anchor ice from forming and prevent super-cooling of the water. By storing spring and summer storm run-off, beaver ponds help to reduce downstream flooding and the damage from rapid increases in stream flows [385].

Beavers also help shape riparian habitat. Beaver ponds increase the surface area of water several hundred times and thereby enhance the overall riparian habitat development [385]. They also enhance vegetation growth by increasing the amount of groundwater for use by riparian plants and wetland areas. The presence of beaver can have both positive and negative influence on salmon habitat, but on the whole, their presence is considered of great benefit to both water quality and salmon, particularly juvenile coho salmon and cutthroat trout, and to many other species of wildlife and invertebrates.

ESTUARY HABITAT

By definition [413], an estuary is a region where salt water of the ocean is measurably diluted by freshwater runoff from the land within a constricted body of water. Thus, the salinity gradient that juvenile salmon encounter when migrating through estuaries depends upon the inflow of fresh water and the strength of the tides, which influences the degree of mixing, and the depth to which the juvenile salmon penetrate the water column. Because the saline seawater is more dense than fresh water from the river, the fresh water tends to lay over the seawater unless it is throughly mixed by tidal, river and wind energies. In the Pacific Northwest, river flow plays a strong role in the structure and dynamics of estuarine circulation [515]. Variation in circulation reflects the general seasonal cycles of the Pacific Northwest climate, but also the geomorphic structure of both watershed and estuary. Estuaries of lowland watersheds along the Washington and Oregon coasts tend to exhibit high peak flows associated with winter storms, but often extremely low flows associated with the dry summers. This can often cause dramatic differences in the available estuarine habitat between winter and spring-summer periods, limiting summer rearing. In some southern Oregon and northern California estuaries river, flow can decrease to the point that bars form across the estuaries' entrances, restricting juvenile salmon ocean emigration to extreme high (spring) tides.

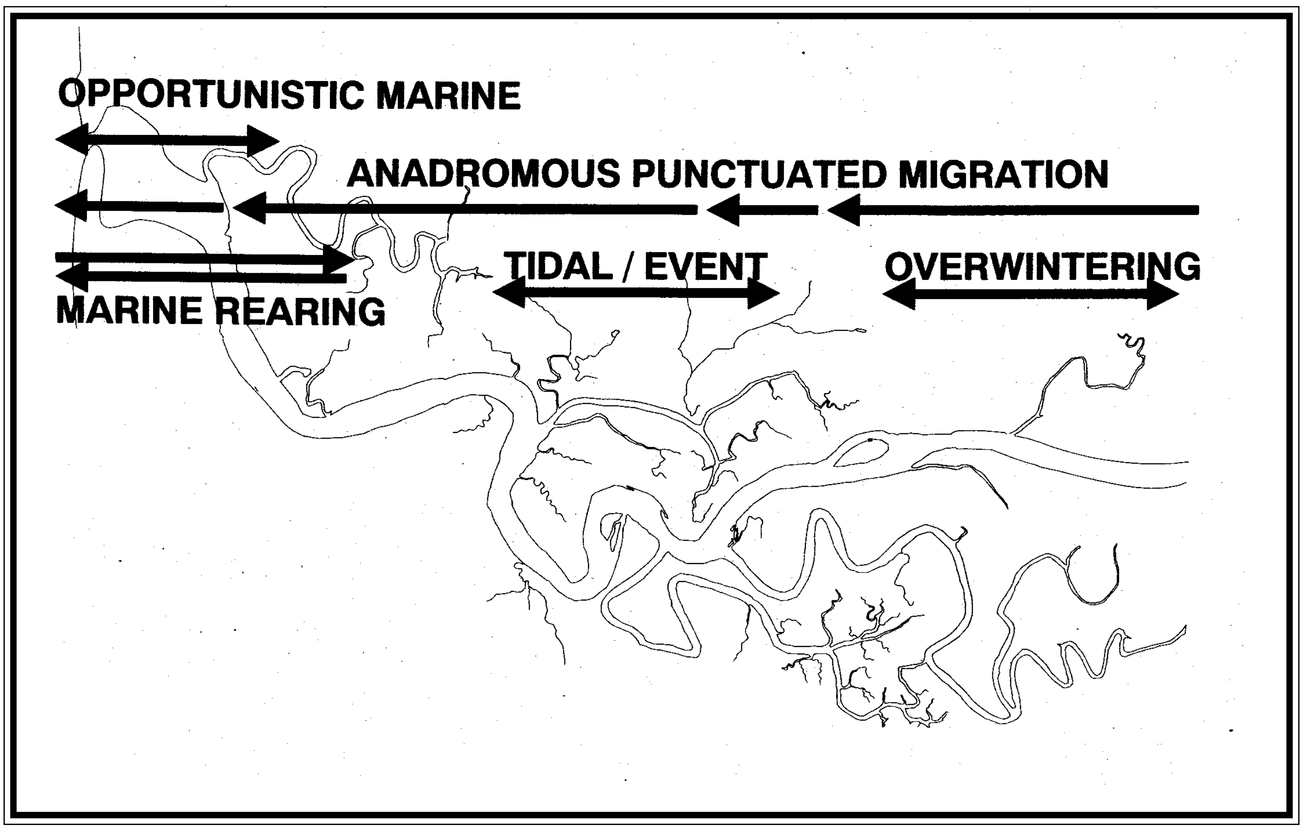
Perhaps the most fundamental concept in understanding the estuarine ecology of juvenile salmon is that the salmon do not respond to singular habitats *per se*, but rather interact with a landscape mosaic of habitats in response to changing migratory mandates, tidal cycles and freshwater runoff events (Figure 6). River flow and tide, physiological change, prey and predator distributions, and likely metapopulation genetic structure as well, all affect the rate of movement through the estuary. But, the opportunity for juvenile salmon to exploit preferred habitats is just as likely dependent on the arrangement of key landscape features such as tidal-freshwater and brackish rearing zones, low-velocity refugia, migratory corridors and foraging patches. Although this is a relatively new topic of research, with few definitive experiments and tests, there is some emerging evidence that the edge of marsh vegetation in dendritic tidal channel and slough systems may relate directly to juvenile salmon production [473].

Large watersheds with significant snow accumulations at higher elevations, and extended melting periods can create prolonged spring freshets [308]. Spring and winter freshets, and winter "rain-on-snow" events associated with rapid snowmelt, produce flooding in tidal floodplains and estuaries that influences short-term and long-term productivity of juvenile salmon and their ecosystems [360, 566]. Although flood plain and estuarine wetland flooding increases flows in the main distributary channels, likely diminishing the ability of juvenile salmon to occupy them, considerable side-channel and other flood plain wetlands (i.e., ponds, relict side-channels) are inundated and become available for refuge and rearing. This flooding recruits organic detritus and dissolved nutrients from these peripheral wetlands and imports them to the estuary. While trapped in estuarine wetlands or circulation features such as estuarine turbidity maxima [472], these materials contribute to primary and secondary production by supporting food web pathways to juvenile salmon.

The structure of the watershed and estuary, and the seasonal variability in river flow, shapes estuarine circulation, and strongly influences juvenile salmon residence time, habitat use and production. Except where the river has been extensively diked and channeled, the flood plain in the freshwater-tidal region is characterized by extreme habitat complexity, abrupt changes in water velocity and low-velocity off-channel habitats. As the "estuarine gateway," the tidal-freshwater mixing zone can be exceedingly important to juvenile salmon [469] because it: (1) provides habitat for overwintering chinook, coho and steelhead forced downstream during high river flows; (2) contains complex low-velocity refugia such as off-channel sloughs and LWD; (3) allows migrating juveniles to adapt physiologically as they encounter brackish waters of the upper estuary; (4) drift insects are trapped and concentrated due to flow reversals, providing opportune feeding conditions [523]; and (5) is the first region of estuarine settling of suspended sediments and detritus, which can fuel soft-sediment habitat formation and detritus-based food webs exploited by salmon. River flow and tide, physiological change, prey and predator distributions, and likely metapopulation genetic structure as well, all affect the rate of movement through the estuary.

Estuaries are composed of both discrete and highly integrated habitat complexes and their associated plant and animal communities. Categorizing habitats to a large degree is a function of scale, as juvenile salmon can respond to habitat features (e.g., LWD or tidal channels) that are elemental to the broader habitats. Estuaries generally posses eight habitat components: (1) subtidal distributaries; (2) mud- and sand-flats; (3) gravel-cobble beaches; (4) low elevation emergent marshes; (5) high elevation emergent marshes; (6) forested and shrub swamps; (7) eelgrass; and (8) kelp. Salmon communities have been shown to utilize many of these habitat types. Juvenile coho (fry, fingerling) are often found rearing during winter and early spring in the tidal flood plains of many large rivers such as the Chehalis River [323, 472, 471, 470]. These fish are either staging for migration through the estuary or are moving back into freshwater for extended rearing. Work in British Columbia [522, 523, 438] and Alaska [512] show that certain sub-populations have a minimal juvenile freshwater rearing phase of their life history ("ocean-type"), and spend extended periods of time either feeding in estuaries or in the ocean. Such subyearling migrant coho, may constitute significant portions (up to 50%) of the returning adult spawners [523].

Figure 6. Movements and migrations of juvenile Pacific salmon across tidal-freshwater delta-estuarine landscapes (Contributed by Simenstad, unpublished diagram).



Natural disturbance regimes are responsible for creating and maintaining habitat complexes important to juvenile salmon. Erosive flooding, channel reconfiguration, and changes imposed by LWD all promote increased habitat complexity and heterogeneity. In the absence of disturbance, early successional habitats such as mudflats and low elevation estuarine marshes (e.g., *Carex lyngbyei* sedge) would not persist or would be relatively rare. Yet, these habitats can be some of the most productive and beneficial of salmon habitats and play unique roles for some salmon species.

Association with specific migratory and rearing habitats in estuaries tends to relate primarily to fish size, but there may be some indications of co-evolutionary habitat partitioning [196, 466]. Juvenile salmon measuring 30-60 mm long tend to occupy near shore shallow water (1-2 m deep), often irrespective of habitat type and tidal stage. The result is that juvenile salmon likely use shallow water habitats as refugia during both migration and rearing. Chum and chinook fry are particularly noted to occupy estuarine marshes and adjoining habitats for extended periods of time, up to 1 month [273, 104, 460]. However, some species diverge from this habitat use: pink fry spend relatively little time in estuarine marshes and start making the transition to more offshore neritic (surface) waters after only a few days to a week in the estuary. In contrast, chum fry do not begin to disperse into neritic habitat until they have grown to 50-60 mm long, which usually involves more than two weeks in the estuary. Based on evidence of extended residence times in estuary habitats, subyearling chinook fry appear to maintain some affinity for shallow-water habitats until they are even larger (i.e., 80-100 mm long) [104, 196, 197]. Information on residence time of coho fry in estuaries is more limited, but residence times for these "ocean-type" fish appear to fall between chum and chinook.

Chum and pink salmon that migrate directly into brackish and saline estuarine waters appear to require little or no interim adaptation [256]; when smoltification does occur, it occurs very rapidly upon entering brackish waters, and adaptability may actually decrease with freshwater rearing [227, 192]. Yearling chinook, coho and sockeye salmon proceed through a definitive smolt stage before entering saline waters, while subyearling chinook and coho appear to spend considerable time in the tidal freshwater-brackish zone of estuaries, perhaps in part due to an extended smoltification process.

Feeding behavior and diet of juvenile salmon passing through and rearing in estuaries is often specialized on specific types, species, and even life history stages of organisms, suggesting strong co-adaptive development of preference for bioenergetically "optimum" prey resources that through rapid growth provides a survival margin upon entry to the ocean [247]. Diet is strongly structured by size of fish and habitat occupied, and to some degree may be influenced by earlier life history stages [466]. The density of prey taxa may actually influence estuarine migration rates and residence times [467, 565].

OCEAN HABITAT

Upwelling along the coast of the Pacific Northwest often results in high primary and secondary productivity, resulting in large standing stocks of fishes, seabirds, and marine mammals. The coastal upwelling domain extends from British Columbia to Baja California and is located inshore of the equatorial flowing California Current. Coastal upwelling is driven by prevailing northwesterly winds during the spring and summer. Those winds result in offshore displacement of near-shore surface waters and vertical advection of deep, cool and often nutrient-rich waters into the euphotic zone along the coast and into estuaries. Rich blooms of phytoplankton are observed along the coast following episodic upwelling events [514, 286, 501]. Upwelling varies seasonally and over longer annual and semiannual cycles, with intensity generally increasing southward to northern California. Upwelling is most intense in regions of capes such as Cape Blanco in southern Oregon.

There was a strong correlation between the intensity of coastal upwelling and the smolt-to-adult survival of hatchery coho salmon from the Oregon Production Index region south of the Columbia River from 1960 to 1981 [373]. During the late 1970s, however, there was a major change in ocean climate in the North Pacific Ocean, called a regime shift or the Pacific Decadal Oscillation, which was correlated with a sharp decline in the survival of Oregon coho salmon between smolt release years 1975 and 1976 [397, 32, 153]. After this regime shift the production of Oregon coho salmon has usually been low. The relationship between coastal upwelling and coho survival is no longer significant. The reason for this changed relationship is unclear, but is related to weak coastal upwelling, warm sea temperatures, high sea levels, and frequent El Niño events [394]. Upwelling has probably not been effective in injecting nutrient-laden water into the euphotic zone because of the deep lens of overlying warm, nutrient-depleted water along the coast [195, 432]. The persistence of warm, unproductive ocean conditions is a major reason for the decline of many stocks of anadromous fishes along the west coast, and for the very large variability in survival and reproduction of marine birds.

Although the mechanisms that have resulted in poor ocean survival of salmon are speculative, one hypothesis is that weak upwelling results in low growth and poor survival of zooplankton and forage organisms, and impacts juvenile salmon during their critical first summer in the ocean. This lack of forage and the narrow band of cool waters along the coast during weak upwelling years concentrates juvenile salmon near the coast where they are more vulnerable to predation by seabirds, marine mammals and fishes [145]. During warm years predators from southern waters, e.g., Pacific and jack mackerel, invade coastal waters and may either compete with or prey upon juvenile salmon [397, 394].

The principal prey of juvenile salmon off the coast of Oregon and Washington during the spring and summer are fishes and crustaceans [83, 83a, 395]. Salmon in the open ocean forage opportunistically on a diverse assemblage of pelagic organisms. The diets of maturing salmon in the North Pacific Ocean vary among species and sizes of fish, with season and year, and with location and proximity to the coast. Fishes, squids, amphipods, copepods, and pteropods are primary prey [268, 396, 178].

ECOLOGICAL RELATIONSHIPS OF SALMON

Macroinvertebrates

Freshwater Macroinvertebrates And Salmon

Freshwater ecosystems are inhabited by a large variety of macroinvertebrates that play an integral part in the salmon's life history. They include insects, crustaceans, and other forms of macroinvertebrates (larger than 595 microns in their later instars or mature forms). Many species in their aquatic phase have been described from the hyporheic zone, or zone below the surface of the stream bottom [492]. Given the variety of physical habitat across the region's landscape, there is an opportunity for freshwater invertebrate species to form diverse and specialized communities.

Freshwater macroinvertebrates play a significant role in energy pathways of aquatic ecosystems. The consumption of algae, detritus, and bacteria is the basis for transfer of this energy. A few invertebrate species are known to actively derive their food base from higher life forms (e.g., small fish). The food source used by an invertebrate defines what function it performs in this food web.

Structure And Function In Macroinvertebrate Communities

The type and location of food in the aquatic environment consumed by invertebrates determines their functional designation. Headwater streams or heavily canopied streams are dominated by leaf litter input, allochthonous material, which has been linked to significant shredder activity [111, 536]. Shredders comprise a group of aquatic insects that utilize coarse particulate organic matter, such as leaf litter, with a significant dependence on the associated microbial biomass [529]. Portions of a drainage where the riparian canopy opens can result in substantial autochthonous input (periphyton growth), and are consumed by scrapers like the mayfly family Heptageniidae [315]. Lower in a drainage the channel can accumulate large deposits of detritus. Invertebrates distributed here are mainly collector-gathers and may constitute the bulk of juvenile salmon diets [196]. The distribution of dominant food sources throughout a drainage are influenced by a continuum of physical changes as one travels from the steep headwater streams to the relatively low gradient flood plains [529].

Invertebrate community structure in a stream or pond reflects physical characteristics of the living space. Numbers of species in a stream ecosystem are usually greater in physically diverse habitats. Structural attributes like species richness change along a disturbance gradient. Two investigations found that species richness was consistently higher in streams with intermediate disturbance of substrate [116, 519]. The effect of disturbance and physical change over a continuum results in species replacement and sometimes adjustments of the functional characteristics in the community [325].

Physical And Chemical Influences On Macroinvertebrate Distribution

Factors that control distribution and abundance of macroinvertebrates are substrate, current velocity, temperature, predators, and food resources [223]. Substrate heterogeneity often promotes greater species richness [326, 328]. Interstitial spaces in stream gravels can serve as refuge from predators and physical disturbance, and entrap detritus. Water temperature in the interstitial microenvironment can be relatively constant and cooler than the overlying surface water [557].

Early life stages of the salmon can be affected by substrate quality. Factors that favor survival of salmon egg and fry (low levels of fine sands and silts) are coincident with requirements of aquatic invertebrates that have a narrow tolerance range to environmental fluctuations. Protection from natural physical disturbance is important for early life stages of salmon and mobile aquatic invertebrates. Stable stream bottoms during periods of flood or freshet reduce predation on dislodged animals. In some instances, salmon redd construction is a natural disturbance that reduces invertebrate density in localized areas of a stream [324]. This disturbance also opened niche space for other functional groups of aquatic insects, like blackflies, who feed on suspended particles and recolonized quickly along with stonefly nymphs and midge larvae [324]. Other invertebrates that enter the drift behaviorally or unintentionally from substrate disturbance are potential prey items for feeding salmon. Mayfly and stonefly density and richness can be reduced by physical alterations to the stream corridor. These changes may have significant implications to the salmon food base.

Invertebrate drift is either voluntary, a behavioral activity, or coincides with catastrophic stream conditions, especially during floods. Taxonomic groups prominent in behavioral drift are amphipods, Ephemeroptera (mayflies), Plecoptera (stoneflies), Tricoptera (caddisflies), and Simuliidae (blackfly larvae). Later stages of the nymph and larval forms are most active in the diel (24-hour cycle) drift [547]. Behavioral drift occurs with a diel periodicity, typically at two peaks in a 24-hour time frame. Most invertebrates that enter the drift are night-active, with photoperiods as the major cue. Fewer invertebrates are day-active and begin drifting by cues through change in water temperature.

Drifting invertebrates are a food source for certain species of fish that forage in the stream water column. Rader [415] determined that the mayfly genus, *Baetis*, whose drift propensity was high, was a significant food source to juvenile and adult salmon. Other studies indicated that food preference of juvenile fish was related to their abundance and location within the stream channel. Juvenile coho salmon diet varied seasonally depending on the type and abundance of invertebrates, salmon fry, or salmon eggs in the benthos or drift [260].

Significance Of Macroinvertebrate Life Cycles

There are two life strategies characteristic of freshwater macroinvertebrate species [558]. The simpler *hemimetabolous* strategy inherent in stonefly and mayfly species contain an egg, multiple nymph, and adult stages. A few of the stonefly species are long-lived (more than a year) in the aquatic nymphal form. Large-bodied stoneflies found in streams indicate adequate flow in channels that are key to survival of early salmon life stages and to some of the invertebrate fauna they will eventually consume.

The second life strategy contains representatives of the *holometabolous* invertebrates. Midges, blackflies, and caddisflies have egg, larva, pupa, and adult life stages. These types are mostly short-lived having one or many generations per year in a population. Aquatic environments that are seasonally stressed by high temperatures, low dissolved oxygen, or drought are primarily colonized by holometabolous invertebrates. These stressors increase the mortality of early life stages in salmon, but encourage dominance of holometabolous species in the aquatic invertebrate community.

Aquatic Macroinvertebrates As A Food Source For Salmon

Aquatic ecosystems are frequently inhabited by both hemimetabolous and holometabolous macroinvertebrates. The hemimetabolous species richness is greater in mid- to upper-drainage streams and play a larger role in the diet of juvenile chinook [197] and coho salmon [442]. Although holometabolous invertebrates are dominant in lower-drainages, species in the family Chironomidae are present in all habitats and are a significant food source to salmon in early freshwater stages [399, 440, 100]. Invertebrate consumption is based on handleable body size and abundance of individuals. Larval and adult insects are the most common forms of food found in natal areas of the freshwater habitat of salmon, with differential diet preferences exhibited by the shorter (chinook) and longer freshwater (cutthroat) life cycle salmon species. Feeding habits gradually change during downstream migration with the addition of large-bodied prey items. However, a certain component of the diet is comprised of accustomed food sources like Chironomidae that were consumed during the early freshwater life cycle.

All species of salmon fry consume some life stages of dipterans, primarily Chironomidae, during the freshwater life phase [178]. Stonefly and mayfly nymphs are consumed by pink, chum, and chinook salmon fry. Coho fry are suspension and surface feeders whose diet is predominately terrestrial insects. Ecologically important freshwater invertebrates in coho natal habitat are emergent and flying insects such as mayflies, stoneflies, and midges (Chironomidae). The rapid migration of chinook fry to the river estuary introduces terrestrial homopterans (leaf hoppers and aphids) into their diet. Additional details of prey items during the freshwater cycle can be found in Simenstad et al. [466], Shreffler et al. [461], Scott and Crossman [449], Chapman and Bjornn [95], Mundie [338], Martin [294], Peterson [399], Friesen [155] and Groot and Margolis [178]. The influence of riparian vegetation along streams and estuaries appears to be an important factor in determining abundance and type of terrestrial insects on which salmon are able to forage.

Salmon as a Food Source For Aquatic Macroinvertebrates

Freshwater macroinvertebrates such as caddisflies, stoneflies, and midges are involved in processing the microbially conditioned salmon carcasses. Bilby et al. [47] observed a significant contribution

Plate #12. Aquatic insects feeding on salmon carcasses. (Photo by: Jason Walter and Brian Fransen).

of nitrogen from spawning salmon to the collector-gatherer invertebrate community. Increases in aquatic invertebrate density from the introduction of salmon carcasses [564] stimulated feeding by early life stages of select salmon species [48]. Other stages of the salmon life history contribute to the invertebrate food base. Nicola [376] observed the stonefly nymph, *Alloperla* (Plecoptera), scavenging dead pink and chum salmon embryos and alevins. Also, Elliott and Bartoo [131] found the midge, *Polypedilum* (Diptera), associated with dead pink salmon embryos and alevins.

Freshwater invertebrate shredder abundance increases in the presence of salmon carcasses [564]. Non salmon-bearing streams support a limited abundance of shredders mediated through input of leaf matter. This organic food base must first be conditioned by the microbial community to increase palatability to shredders. Cool water temperatures characteristic of coastal streams slow the microbial decay of the leaf litter food source resulting in limitations in distribution and abundance of the shredder community. The appearance of salmon and the additional influx of biomass to streams appears to be a controlling factor for shredder species. However, the role of shredders in the presence of salmon carcasses continues to be investigated. Bilby et al. [47] found no significant concentrations of carbon contributed from decaying carcasses in the shredder community. Undigestable animal tissue consumed by shredders was excreted as fine particulate organic matter. Nutritive food value for shredders may have been derived primarily from the microbial community on decaying carcasses. Aquatic insects of the collector-gatherers group typically benefit from the activity of shredders [316, 47].

The relationship between invertebrates and salmon can be complex. Functions of invertebrates have not yet been fully defined, but we know they are essential to salmon survival. Traditional functional groupings of invertebrates have been helpful in understanding their ecological roles; however, continuing research suggests that many genera are capable of filling other functional groups if given the opportunity and resources (Plotrikoff, personal communication). Invertebrates complete a loop beginning as recipients of food from adult salmon carcasses that, in turn, fuel the growth and survival of early stages in the salmon's life cycle.

Vertebrate Wildlife

Vertebrate Wildlife And Salmon

Anadromous salmon provide a rich, seasonal food resource that directly affects the ecology of both aquatic and terrestrial consumers, and indirectly affects the entire food-web that knits the water and land together. Wildlife species have likely had a very long, and probably co-evolutionary, relationship with salmon in the Pacific Northwest. In their *Natural History of Washington Territory and Oregon*, Suckley and Cooper [502] wrote of the California condor:

> *"The Californian vulture visits the Columbia river in fall, when its shores are lined with great numbers of dead salmon, on which this and the other vultures, besides crows, ravens, and many quadrupeds, feast for a couple of months."*

The "Five Mile Rapids" prehistoric archaeological site along the banks of the Columbia River, five miles east of the Dalles, Oregon, yielded bones from at least 63 individual California condors, plus remains of turkey vultures, cormorants, bald eagles, and gulls [110]. Carbon-14 dating placed materials at this site from 10,000 to 7,500 years before present [323, 474]. Miller [321] suggested that these birds were attracted to the site by the presence of abundant living and dead salmon and human refuse resulting from fishing.

The life stages of salmon (i.e., eggs, fry, smolts, adults, and carcasses) all provide direct or indirect foraging opportunities for terrestrial, freshwater, and marine wildlife. While sometimes abundant and somewhat dependable from year to year, the availability of salmon to wildlife is largely seasonal in nature. The high seasonal variability in a particular food resource is reflected in the opportunistic foraging of many wildlife consumers - however, "opportunistic" is not a synonym for biological unimportance. Thus, one could hypothesize that while many wildlife species could develop important food-web relationships with salmon, few wildlife species would likely be able to form an ecological "dependance" on salmon. Only those species which are highly mobile, or are able to capture, consume, and store (in body tissues) substantial quantities of salmon biomass in a short period of time would be likely to develop a strong direct ecological dependence on salmon. It is more probable that the majority of wildlife which directly consume salmon will have flexible foraging strategies, utilizing salmon when available, and alternate food sources during other times of the year.

Indirect relationships develop when a food resource is providing foraging opportunities to a secondary consumer, an example in our case is reflected by peregrine falcons which eat gulls that feed on salmon carcasses. As salmon are a concentrated resource, this will serve to concentrate otherwise dispersed wildlife species (e.g., bears). In this scenario, there may well be competition, parasitism, or other aggressive interactions between or among wildlife species. Some of these interactions, e.g., bald eagles disturbing common mergansers, serve to benefit salmon by reducing predation. The magnitude of the salmon-wildlife interaction warrants special examination and calls attention to the pervasive occurrence of these important ecological functions linkages across the region. The loss or severe depletion of anadromous fish stocks could have major effects on the population biology (i.e., age class, longevity, dispersal ability) of many species of wildlife, and thus, on the overall health and functioning of natural communities over the majority of the region.

Research on predator-prey interactions in which anadromous fish are the prey has strongly emphasized the effects of predation on the fish populations [576, 570, 571, 559, 331, 430, 225]. Many existing studies describe predatory species as competitors of human harvesters and attempt to control the rate of predation to maximize human consumption. Focusing on the important interplay between salmon and wildlife populations will help to reverse this perspective. In the following sections, we discuss the relationships between salmon and their vertebrate consumers, and the salmon's role in enhancing ecological functions involving wildlife in terrestrial, freshwater, and marine systems.

Wildlife Species With A Relationship To Salmon

Johnson et al. [233] examined the relationships between the Pacific salmon and 605 species of terrestrial and marine mammals, birds, reptiles, and amphibians currently or historically common to Washington and Oregon. They found a positive relationship between salmon and 138 species of wildlife, the relationship was "unknown" for 60 species, and a determination of "no relationship" was made for 407 species (Table 3). Where a relationship existed, they identified both the type(s) of relationship and the stage(s) of the salmon life cycle to which it applied. Of the 138 species with a relationship to salmon, 9 species were categorized as having a *Strong, Consistent* relationship (Appendix I), 58 as *Recurrent* (Appendix II), 25 as *Indirect* (Appendix III), and 65 as *Rare* (Appendix IV). This tally totals more than 138 because 19 species had more than one type of relationship with salmon.

Of the 138 wildlife species, 88 were characterized as having a <u>routine</u> relationship (combination of species with *Strong, Consistent, Recurrent;* and *Indirect*) with salmon. Of these 88 species, there were 25 mammals (8 of these were marine mammals), 60 birds, 2 amphibians, and 1 reptile.

The relationship categories are briefly described as follows:

1) *Strong, Consistent Relationship.* Salmon play (or historically played) an important role in this species distribution, viability, abundance, and/or population status. The ecology of this wildlife species is supported by salmon, especially at particular life stages or during specific seasons. Timing of reproductive activities, and daily or seasonal movements often reflect salmon life stages. Relationship with salmon is direct (e.g., feeds on salmon, or salmon eggs) and routine. The relationship may be regional or localized to one or more watersheds. Examples: A significant portion of the diet of killer whales is adult salmon (*Saltwater* stage); common mergansers may congregate to feed on salmon fry (*Freshwater Rearing* stage) when they are available.

2) *Recurrent Relationship.* The relationship between salmon and this species is characterized as routine, albeit occasional, and often tends to be in localized areas (thus affecting only a small portion of this species population). While the species may benefit from this relationship, it is generally not considered to affect the distribution, abundance, viability, or population status of this species. The percent of salmon in the diet of these wildlife species may vary from 5% to over 50%, depending on the location and time of year. Example: turkey vultures routinely feed on salmon carcasses, but feed on many other items as well.

3) *Indirect Relationship.* Salmon play an important routine, but *indirect* link to this species. The relationship could be viewed as one of a secondary consumer of salmon; for example, salmon support other wildlife that are prey of this species. This includes aspects such as salmon carcasses that support insect populations that are a food item for this species. Example: American dippers feed on aquatic insects that are affected by salmon-derived nutrients. The hypothesis of an *indirect* relationship between an aerial insectivore and salmon was supported by the presence of two or more of the following characteristics of the insectivore: (1) riparian obligate or associate, (2) feeds below or near the canopy layer of riparian trees, (3) known or perceived to feed on midges, blackflies, caddisflies, stoneflies, or other aquatic insects that benefit from salmon-derived nutrients, and/or (4) feeds near the water surface. While this category includes general aspects of salmon nutrient cycling in stream/river systems, we are not including or examining the role of carcass-derived nutrient cycling on lentic system riparian and wetlands vegetation, and subsequent links to wildlife.

4) *Rare Relationship*. Salmon play a very minor role in the diet of these species, often amounting to less than 1 percent of the diet. Typically, salmon are consumed only on rare occasions, during a shortage of the usual food and may be especially evident during El Niño events. As salmon are often present in large quantities, they may be consumed on rare occasions by species that normally do not consume them. Examples: red-tailed hawks are known to consume salmon carcasses in times of distress; trumpeter swans are primarily vegetarians, but on rare occasions will consume eggs, parr, as well as salmon carcass tissue.

5) *Unknown Relationship.* A relationship between this species and salmon may exist, but there is not enough information to determine the scope or scale of the relationship at this time. Example: while it is logical to speculate that riparian feeding bats may feed on salmon-derived insects, aspects of seasonality of both bats and salmon carcasses are relevant, as is the nocturnal flight behavior of the insects. Do bats and salmon carcasses coincide seasonally, and if so, are salmon-derived insects actually available to feeding bats? At this time, the evidence for this relationship is inconclusive and remains to be examined.

6) No Relationship. There is no recognized or apparent relationship between salmon and this species.

As part of the same study, Johnson et al. [233] reported 60 species as having an "unknown" relationship with salmon (Appendix V), suggesting that the diets of these species *in Washington and Oregon*, were not understood well enough to characterize their relationship with salmon. Additional observations on the diets of these species will help determine whether the relationships of these species with salmon is routine, a rare and unusual event, or whether a relationship exists at all. Johnson et al. [233] identified 407 species as having “no relationship” to salmon (Appendix VI).

able 3. Relationship between Pacific salmon and 605 species of wildlife in Washington and Oregon. here were 137 species with a positive relationship with salmon (i.e., combined total for species with *Strong, Consistent, Recurrent, Indirect*, and *Rare* relationships). The total number of individual wildlife species for columns and rows are shown in parenthesis; the number of species shown in the rows and columns may not equate to the numbers shown as totals as 19 species had more than one type of relationship with salmon, and 73 species are associated with salmon at more than one life stage.

Salmon life stage	*Strong, Consistent* relationship	*Recurrent* relationship	*Indirect* relationship	*Rare* relationship	*Unknown* relationship	*No* relationship
Incubation - eggs and alevin (23)	2	10	1	10		
Freshwater Rearing - fry, fingerling, parr (49)	4	31	4	10		
Saltwater - smolts, immature adults, adults (63)	6	36	5	19		
Spawning (16)	5	10	0	1		
Carcasses (82)	5	28	22	38		
	(9)	(58)	(25)	(64)	(60)	(408)

Wildlife Response To Salmon Congregations

The numerical response of predators to salmon congregations is often substantial, sometimes spectacularly so. The ability of wildlife species to concentrate at salmon sites is more than opportunistic foraging, it has significant biological importance. Anadromous fishes (including their eggs) are a major source of high-energy food that allows for successful reproduction and enhanced survival of adults and juveniles of many wildlife species, and support for long-distance migrant birds. Wildlife movements to salmon congregations can be seasonal (e.g., bald eagles along the Skagit River in Washington), or depending on the situation (e.g., hatchery fish released during an El Niño high food-stress seabird breeding season) can occur within a matter of hours. Perhaps as noteworthy, but much harder to detect, is that some wildlife species that have been reported to group at salmon sites in other areas (e.g., black bears in southeast Alaska) do not appear to be doing so with any regularity in Washington and Oregon. This may well be reflecting the depressed nature of some salmon stocks rather than the inherent behavior of the wildlife species. Of the 88 species with a link to salmon [233], 43 species (37 birds, 6 mammals) concentrate or form loose aggregations at salmon sites (Table 4). Some reasons why other species do not congregate at salmon streams are: strong territoriality (e.g., great blue heron), foraging strategies which require above-water structures or perches (e.g., belted kingfisher), and limited movement capabilities (e.g., shrews).

Table 4. Wildlife species that have been observed or are perceived to aggregate at salmon congregations in Oregon and Washington.

Western grebe	Western gull	Bald eagle
Clark’s grebe	Glaucous gull	Tree swallow
Common Goldeneye	Glaucous-winged gull	Violet-green swallow
Barrow’s Goldeneye	Ring-billed gull	Northern rough-winged swallow
American white pelican	Herring gull	Bank swallow
Brown pelican	California gull	Cliff swallow
Brandt’s cormorant	Thayer’s gull	Barn swallow
Double-crested cormorant	Rhinoceros auklet	Northern (Steller) sea lion
Common merganser	Tufted puffin	California sea lion
Red-breasted merganser	Common murre	Harbor seal
Elegant tern	Black-billed magpie	Killer whale
Common tern	American crow	Black bear (now questionable)
Caspian tern	Northwestern crow	Grizzly bear (now questionable; may not be enough salmon available to congregate at)
Arctic tern	Common raven	
Forester’s tern	Turkey vulture	

That some wildlife species concentrate at salmon areas is well established. The fact that other wildlife species do not concentrate at salmon areas may reflect salmon declines. We offer the following examples relevant for Washington and Oregon.

Bald Eagle Suckley and Cooper [502] state: *"This noble looking bird is exceedingly abundant in Oregon and Washington Territories, and in certain localities, especially during the salmon season, may be found in great numbers."* The North Fork of the Nooksack River (coastal Washington) currently hosts one of the largest and most visible concentrations of wintering bald eagles in the lower forty-eight states. Peak concentrations (100 or more eagles) occur along the Nooksack [263] and Skagit [218] rivers with December- and January-spawning chum salmon.

Caspian Tern The first breeding record of Caspian terns along the Oregon/Washington coast was a colony of 50 pairs in Grays Harbor, Washington in 1957 [6]. This, and other nesting colonies (mid-1950's through early 1990's) along the Washington coast in Grays Harbor, Willapa Bay, and near the mouth of the Columbia River, have been abandoned or destroyed by human actions [429, 430, 479]. A colony of Caspian terns originally settled on Rice Island, a dredge material disposal island in the lower Columbia River, in 1987. In 1997, an estimated 14,000 terns used this island for nesting and/or roosting during the 80-100 day (April-July) breeding season [429, 430]. This represents the largest known colony of Caspian terns in North America, and possibly the world. In 1997, the terns appeared to be largely dependent on juvenile salmon (roughly 75% of the diet), consuming an estimated 14.5 million smolts, the majority being hatchery fish [429, 430]. Tern nesting success was very low (roughly 5%) in 1997; predation on adult terns by bald eagles, and gull predation on tern eggs and chicks (caused by eagle and researcher disturbance) were the primary causes [429, 430].

Common Murre The common murre is a seabird that nests in large colonies along the Oregon coast; colonies in Washington have undergone significant declines in the last decade. It is only an occasional consumer of salmon, as the vast majority of its diet is other small marine fishes. A severe El Niño event occurred in 1983 during the seabird nesting season along the eastern Pacific coast, with the majority of common murres (and other seabirds species) either not attempting to nest or abandoning their nests once initiated [27, 210]. Adult survival was also greatly reduced [169]. Oregon Aqua-Foods, Inc. had released a total of 2 million or more salmon smolts into the Yaquina Estuary at roughly 2.5 day intervals between June and August since 1977 [28]. Murres were more numerous at the mouth of Yaquina Estuary for the first two days post-release in July of 1983 than in July of 1982 (a non-El Niño year), as they were drawn in to feed on the released salmon. First day post-release averages of murres were 3,710 in 1983 and 3,053 in 1982. In August of 1983 however, murre numbers were significantly lower than in 1982 (average 1983 = 106; 1982 = 1,860) , as murres had begun moving north earlier to feed on other food resources [27]. In summary, although not a primary food resource, murres will make use of salmon resources during food-stress conditions.

Black Bear Contrary to popular image, Washington and Oregon black bears rarely congregate at salmon sites. Poelker and Hartwell [406] reported on three diet studies of black bears in western Washington for the time periods of 1952-54 and 1968, and found that fish represented 5.0% of the diet. In their treatise on land mammals, Verts and Carraway [535] describe black bears in Oregon as being largely herbivorous, and do not mention salmon as part of their diets. Cederholm et al. [91] found black bears on Washington's Olympic Peninsula to heavily consume salmon carcasses. In northern California, Kellyhouse [244] found evidence of salmon in 10% of black bear fecal samples analyzed from spawning areas. The California Department of

Fish and Game [84] also reported black bears taking advantage of anadromous fish runs. The strong link between black bears and salmon was demonstrated in the Anas Creek drainage of southeastern Alaska (D. Chi, personnal communication). This effort studied the behavior and activity patterns of black bears (n = 40 individuals) which had established movement patterns according to salmon migrations. Bears arrived in the lower reaches of the creek in June to begin feeding on spawning salmon, and stayed through August and early September to feed on salmon carcasses. Thirteen of the bears were radio-marked and their movements indicated that they were moving in from at least eight miles (12.9 km) away. Other bears were assumed to be coming in from further away. The general lack of salmon in the published accounts of black bear diets across Washington and Oregon [exception: see 91] is somewhat counter to the observed salmon use in adjacent regions. Radio-marked bears in Washington (G. Kohler, personnal communication) and Oregon [528] have been found to move to and congregate at higher elevations in the fall to feed on huckleberries (i.e., forming "traditional use areas"), thus, one could reasonably conclude that if salmon were to be found in substantial and predictable numbers, bears in Washington and Oregon, like those studied by Chi in Alaska, would also establish traditional use areas around salmon. Black bears in western Washington typically den by 1 November and emerge around 1 April, thus salmon runs occurring during the winter will not be available to bears. Recent bear studies in western Washington have included the Humptulips, Wishkah, Wynoochee, and Quinault Rivers and while these rivers hold low levels of hatchery-based salmon, bears do not congregate along them (G. Kohler, personnal communication). D.H. Johnson (unpublished data) summarized 1990-1998 hatchery return data of adult salmon for the Humptulips river system in western Washington. These fish return to the hatchery facility as early as late-September (most begin around mid-October), and as typical with most, were done spawning by mid-December. While there are additional fish in this system, an average number of 217 (range 95-320) chinook, 6,496 (range 177-10,195) coho, and 165 (range 51-339) steelhead returned annually to the hatchery. The substantial majority of these fish species return to spawn after November 1st (the average date of bear denning) and are not available to bears; an average of 73 chinook, 1,264 coho, and 0 (zero) returning steelhead were available to black bears. Here, "available" means simply present in the river system, and not located at spawning redds. In summary, bears have a strong relationship to salmon where they have access to them, but it appears that in substantial measure, current salmon populations do not represent a predictable food supply to bears in Washington and Oregon.

Review Of Wildlife Relationships By Salmon Life Stages

For the 138 species with a relationship to salmon, Johnson et al. [233] identified the salmon life stage(s) involved for each species. In this study, the five general life history stages of salmon were identified as: (a) *Incubation* (egg and alevin), (b) *Freshwater Rearing* (fry, fingerling, and parr), (c) *Saltwater* (smolt, subadult, adult), (d) *Spawner*, and (e) *Carcass*. The number of wildlife species associated with each (in parenthesis) were: *Incubation* (23), *Freshwater Rearing* (49), *Saltwater* (63), *Spawning* (16), and *Carcass* (83); this tally of wildlife species totals more than 138 because 73 species are associated with salmon at more than one life stage (Appendixes I, II, III). See Appendix VII for a complete list of published and unpublished observations of wildlife predators and scavengers on salmon at various stages of their life.

Incubation Stage (eggs and alevin)

Twenty-three wildlife species are linked to salmon at this stage. Twenty-two wildlife species are direct consumers of "drift eggs" (eggs not buried in redds) or alevin (2 amphibians, 1 reptile, 19 birds, and 1 mammal); and 1 bird (bald eagle) is an indirect consumer of eggs/alevin, feeding on the waterfowl that consume eggs and alevin.

Freshwater Rearing (fry, fingerling, and parr)
Forty-nine wildlife species are linked to rearing salmon, including 2 amphibians, 5 reptiles, 34 birds, and 4 mammals. Forty-five of these species are direct consumers of salmon and 4 species (bald eagle, gyrfalcon, peregrine falcon, and snowy owl) are indirect consumers, feeding on terns, waterfowl, gulls, and other animals that eat rearing salmon.

Plate #13. Garter snake eating a salmon smolt, unknown Olympic Peninsula stream, Washington. (Photo by: Jim Rozell, deceased).

Saltwater (smolt, subadult, adult)
Sixty-three wildlife species are consumers of salmon at this stage (51 birds and 12 marine mammals). Fifty-eight of these species are direct consumers of salmon and 5 species are indirect consumers. This list is somewhat expansive due to the geography being included, that is, the estuarine and all marine water habitats.

Spawner
Sixteen species of wildlife are consumers of spawning salmon (6 birds and 10 mammals). This list is relatively small, as few wildlife species are physically capable of capturing and handling live, adult fish. The gray wolf and grizzly bear are on this list, but both have undergone significant range contractions and declines in their abundance (e.g., both are extirpated from Oregon and significantly reduced in Washington).

Plate #14. River otter, a known predator of salmon. (Photo by: Charles J. Gibilisco).

Carcass

Carcasses are linked to the largest group of wildlife consumers of any salmon life stage, with 83 species (1 reptile, 50 birds, and 32 mammals) being consumers of carcasses and/or carcass-derived insects. Body sizes of these animals range from shrews to grizzly bears. Seventy-one species of wildlife (1 reptile, 38 birds, and 32 mammals) are direct consumers of carcasses; 22 species (14 birds and 8 mammals) are consumers of carcass-derived insects; and 10 species (2 birds and 8 mammals) are consumers of both carcasses and carcass-derived insects.

Plate #15. Gull eating a chum salmon (O. keta) carcass at Kennedy Creek, Washington. (Photo by: Jeff Cederholm).

Plate #16. Pacific Giant Salamander, a known predator of juvenile salmon. (Photo by: William Leonard).

Continued documentation of wildlife species-salmon interactions, especially of the 60 species having an “unknown” relationship, will provide vital information for ongoing developments in ecologically-based salmon spawner escapement research and prescriptions for riparian management practices. As Key Ecological Functions (KEFs) are identified through such research [292], tools for informed decisions will be made available to fish and land managers operating under an ecosystem context.

See Appendix VII for a complete list of published and unpublished obervations of wildlife predation and scavenging on salmon at various stages of their life.

Key Ecological Functions (KEFs) Provided To The Ecosystems Through Salmon-Wildlife Interactions

In striving to manage for healthy and sustainable ecosystems, we simultaneously are striving to provide for the full range of ecological functions that these systems provide. Key ecological functions (KEFs) refer to the main ecological roles of a species (or group of species) that influence diversity, productivity, or sustainability of ecosystems [334]. A given KEF can be provided by a single species or shared by many species, and a given species can have several KEFs. Main categories of KEFs include trophic relations; herbivory; nutrient cycling; interspecies relations; disease; pathogen and parasite relations; soil relations; wood relations; water relations; and vegetation structure and composition relations. Building upon work by Marcot et al. [291], Marcot and Vander Heyden [292] characterized the key ecological functions for each of the 605 common wildlife (i.e., terrestrial and marine birds, mammals, reptiles, and amphibians) species in Washington and Oregon. Several questions can be thus posed:

- *In what way does providing for salmon also provide for a wider array of ecological functions of wildlife species associated with salmon?*
- *What are those functions?*
- *How do different kinds of salmon-wildlife relations, and different salmon life stages, provide for an array of ecological functions?*

This somewhat innovative analysis describes the functional links among fish and wildlife species across aquatic and terrestrial communities. To conduct this analysis, we queried the database matrixes on salmon-wildlife relations, key ecological functions of wildlife species, and habitats used by wildlife [236]. The general conclusion is that salmon provide a causal mechanism for movement behaviors and a nutrient source for a variety of wildlife species, which in turn perform a surprisingly broad array of ecological functions [292] across a wide span of habitats. For this analysis, one can think of the array of ecological functions performed by these wildlife species as a “functional web”. It focuses on salmon in their various life stages, and extends well beyond the aquatic realm to influence the diversity, productivity, and ultimately sustainability of habitats and ecosystems throughout Washington and Oregon.

Wildlife With Strong Consistent Links to Salmon

The 9 species of wildlife with strong consistent links to salmon (bald eagle, American black bear, Caspian tern, common merganser, grizzly bear, harlequin duck, killer whale, osprey, and river otter) comprise a functional group of “salmon-eaters” with close affinities to salmon. There are 32 primary wildlife-habitats across Washington and Oregon [236]; Figure 7 summarizes the occurrence of these 9 wildlife species by habitat. Not surprisingly, most of these 9 species inhabit freshwater and marine habitats, but some of them also occur across the range of inland forest, woodland, shrubland, and grassland habitats. It is of interest that from 1-7 of these 9 species can be found in each of the 32 habitats (Figure 7). In this way, salmon provide for a set of wildlife species that occur well beyond just salmon-inhabited aquatic systems.

In addition, the full set of key ecological functions performed by these 9 species also extends beyond the aquatic system. Each of these species provides a set of ecological functions to the various array of habitats that they occur within. Figure 8 depicts the collective range of ecological functions that these 9 wildlife species provide to the number of habitats that they occupy. The functions range from various trophic, organismal, and wood and soil relations. Some functions are more widespread (occur in more habitats)

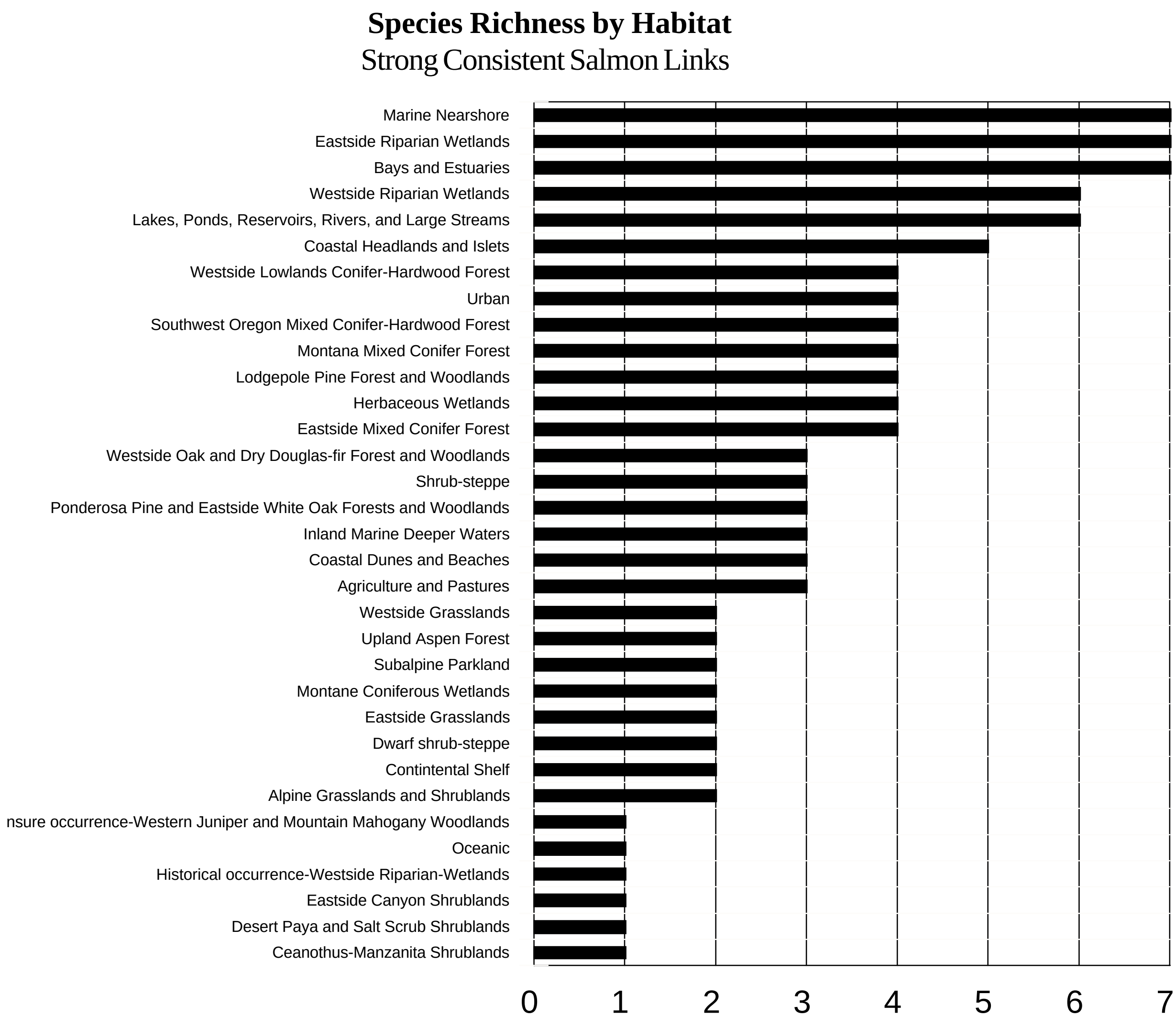


Figure 7: Occurence by number of vertebrate wildlife species in the 32 wildlife habitats in Washington and Oregon, as used by the nine wildlife species with a strong consistent relationship to salmon.

than are other functions. Examples of some widespread functions are potential control of vertebrate populations (through predation), carrion feeding, piscivory (fish-feeding), invertebrate feeding (including insectivory), omnivory, transportation or dispersal of seeds and animals, creation of terrestrial runways used by other species, and secondary use of burrows created by other species.

Species Richness by Function
Strong Consistent Salmon Links

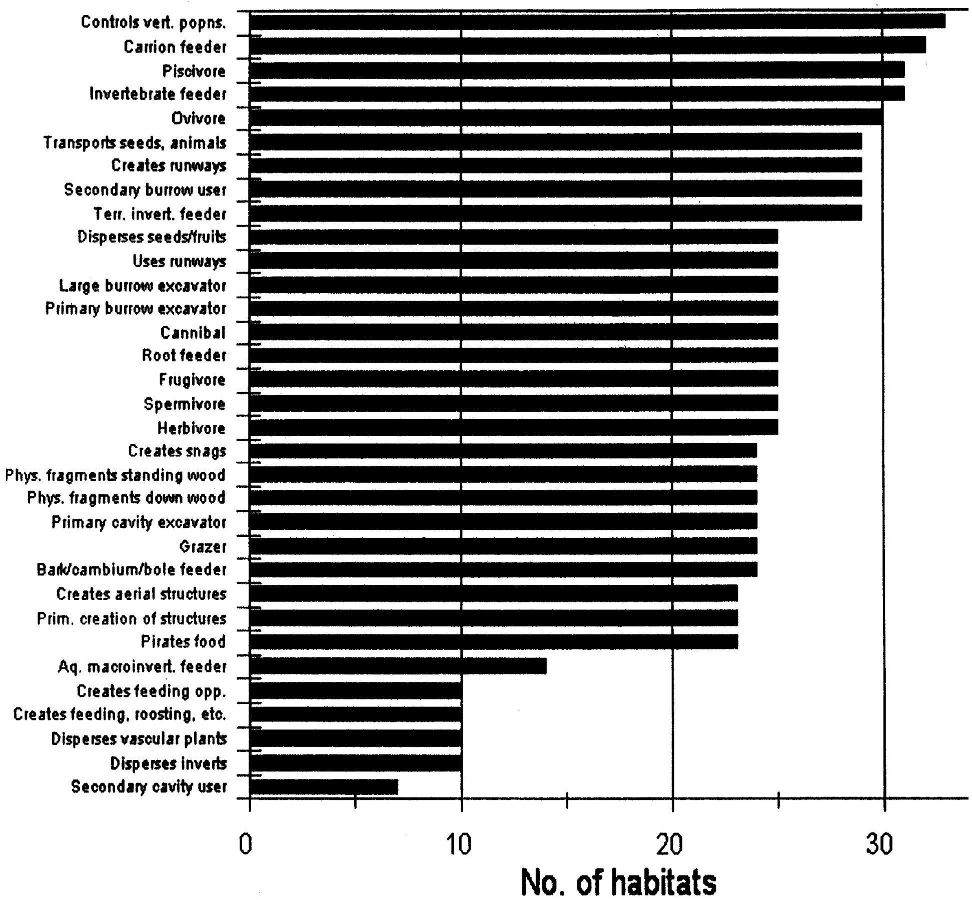


Figure 8: The array of key ecological functions performed by the nine vertebrate wildlife species with a strong, consistent relationship to salmon, across the 32 wildlife habitats in Washington and Oregon.

<u>All Wildlife With Links to Salmon</u>

What of the full set of species showing either strong consistent, recurrent, and/or indirect links to salmon? (Some species have more than one type of relation because they use more than one salmon life stage). Table 5 lists key ecological functions of wildlife more or less unique to each type of salmon-wildlife link. Each of the 3 types of relations provides for some unique set of ecological functions. For example, wildlife species indirectly linked to salmon can provide the following ecological functions: fungivory (fungus-eating), tertiary consumption or secondary predation, prey source; regulate insect populations through predation; serve as interspecific host for avian nest parasites, and create primary small ground burrows. These functions are performed not at all, or by far fewer wildlife species, by the wildlife species with strong consistent links or occasional links to salmon.

Table 5. IMPORTANCE OF TYPES OF SALMON-WILDLIFE RELATIONS TO KEY ECOLOGICAL FUNCTIONS.

1. STRONG CONSISTENT RELATIONSHIPS ARE IMPORTANT FOR:

- trophic relations:
  - primary consumption:
    - spermivory
    - grazing
    - frugivory
    - root feeding
  - organismal relations:
    - controlling vertebrate populations
    - dispersing seeds, fruits, inverts, vac. plants
    - creating feeding opportunities for other species
    - primary cavity excavation in trees and snags
    - primary creation of large ground burrows
    - primary creation and secondary use of ground runways
  - wood relations:
    - fragments standing and down wood
    - kills standing trees (creates snags)

2. OCCASIONAL RELATIONSHIPS ARE IMPORTANT FOR:

- trophic relations:
  - pirating of food
- organismal relations:
  - secondary use of aerial and aquatic structures created by other spp.
- disease relations:
  - carrier of domestic animal disease
- soil relations:
  - improves soil structure and aeration by digging and burrowing

3. INDIRECT RELATIONSHIPS ARE IMPORTANT FOR:

- trophic relations:
  - primary consumption:
    - fungivory
    - tertiary consumption
- prey relations:
  - providing prey for predators
- organismal relations:
  - controlling insect populations
  - serves as interspecific host for avian nest parasite
  - primary creation of small ground burrows

Table 6. IMPORTANCE OF SALMON LIFE STAGES TO KEY ECOLOGICAL FUNCTIONS. (Listed are functions unique to each life stage category.)

1. INCUBATION STAGE IS IMPORTANT FOR:

1. organismal relations:
   - secondary cavity use
   - primary excavation of small ground burrows

2. FRESHWATER REARING STAGE IS IMPORTANT FOR:

(no specific function is mostly supported by this stage)

3. SALTWATER STAGE IS IMPORTANT FOR:

2. organismal relations:
   - creates aerial structures used by other spp.
   - creates aquatic structures used by other spp.

4. SPAWNING STAGE IS IMPORTANT FOR:

3. trophic relations:
4. primary consumption:
   - spermivory
   - grazing
   - frugivory
   - root feeding
   - bark/cambium/bole feeding
5. organismal relations:
   - controlling vertebrate populations
   - creating feeding opportunities for other species
   - primary cavity excavation
   - primary excavation of large ground burrows
   - primary creation of ground runways
   - secondary use of ground runways
6. wood relations:
   - fragments standing and down wood
   - kills standing trees (creates snags)

5. CARCASS STAGE IS IMPORTANT FOR:

7. trophic relations:
8. primary consumption:
   - fungivory
9. organismal relations:
   - controlling insect populations
   - serves as interspecific host for avian nest parasite

What this means is that different degrees of salmon-wildlife relations provide for some unique kinds of wildlife ecological functions. Only the full set of all wildlife-salmon link relations can provide for all collective functions. Thus, to manage the full set of all ecological functions, one should not focus solely on those few wildlife species with strong consistent links to salmon, but on all types of links.

How Salmon Life Stages Provide for Ecological Functions

In a similar way, most of the 5 life stages of salmon provide for a unique set of wildlife species and their ecological functions (Table 6). For example, wildlife associated with the incubation stage of salmon include secondary cavity users and primary excavators of small ground burrows; these two ecological functions are not provided, or only poorly provided, by wildlife species associated with any of the other salmon life stages. Thus, to manage for the full set of ecological functions, one should focus on providing all life stages of salmon.

Managing the Functional Web

So what is the manager to do with this information? For one, be aware that salmon can be viewed as the center of a broad "functional web" of wildlife and their ecological roles. Such roles extend well past the salmon populations and aquatic habitats themselves, and likely influence the structure and processes of the communities and ecosystems in which they reside, thus a "keystone" species [559].

Second, one can use the information presented here and in the species data matrixes to list the collective set of habitat elements and conditions used by wildlife species associated with salmon. For example, one can link the list of wildlife associated with salmon life stages likely to be found in low order headwater streams, and determine the set of habitat elements used by this set of wildlife species, by habitat type, and then establish habitat-specific management guidelines to provide for such habitat elements over time. Maintaining such habitat elements and conditions would help maintain the full salmon-wildlife functional web.

Third, one can begin to predict – or, at least pose tentative management hypotheses about – which ecological functions may be in jeopardy if the wildlife that performs such functions are not maintained. That is, one can now determine which wildlife species may be influenced by altering salmon populations and habitats that imperil specific salmon life stages, and the set of ecological functions associated with such wildlife species. In some cases, other wildlife species not associated with salmon may also perform some ecological function, but never in exactly the same manner and in the same set of habitats and habitat elements.

SALMON FISHERIES

Washington and Oregon salmon fisheries includes commercial, recreational, and treaty harvests that occur in the states' rivers, inland lakes, inland marine waters, coastal embayments, and at sea. Fishing is an important source of mortality, both for immature fish in the ocean and mature fish on their return to freshwater to spawn (Figures 9, 10, 11, 12, 13, and 14). Understanding past fishery effects is important because man's increasing efficiency as a predator augments the natural mortality rates that salmon encounter in natural situations. Because of the presence of humans, salmon are significantly less available to a wide variety of natural consumers in the freshwater, terrestrial,

Plate #17. Commercial salmon fishing vessel. (Photo by: Washington State Historical Society, Tacoma, WA. Curtis. Photo Negative No. 63811).

Plate #18. Steelhead sport catch on the Hoh River, Washington. (Photo by: Jeff Cederholm)

and marine environments, and thus these ecosystems are suffering. According to the NRC [365], salmon mortality caused by human activities and natural factors usually exceed fishing mortality. Thus, although factors other than fishing have a major effect on the production of adult fish, fishing is still the easiest salmon mortality factor to control [365].

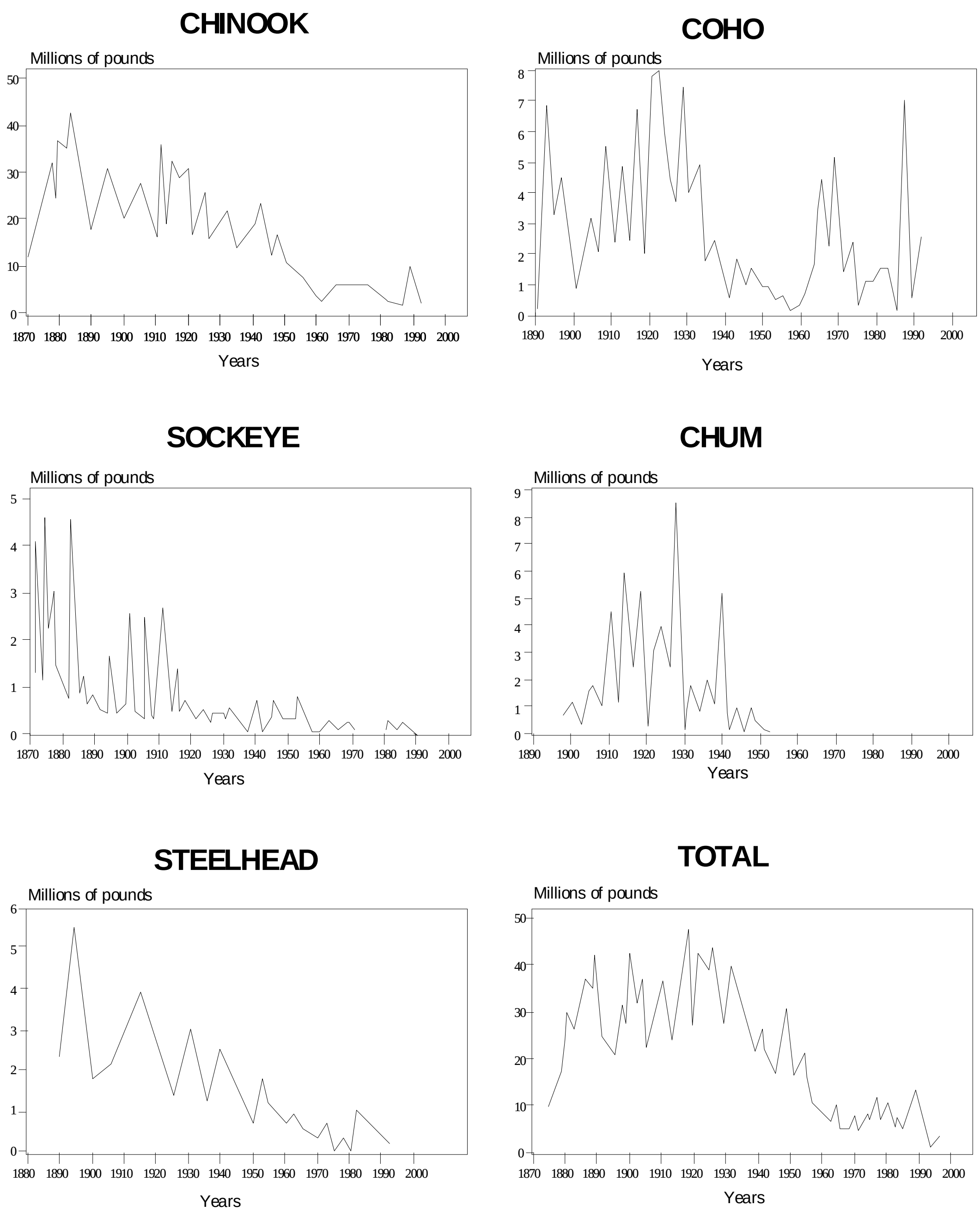


Figure 9. Total commercial catch, in millions of pounds, of Lower Columbia River Salmon from 1870's to 1990's [390, 379, 387b, 540].

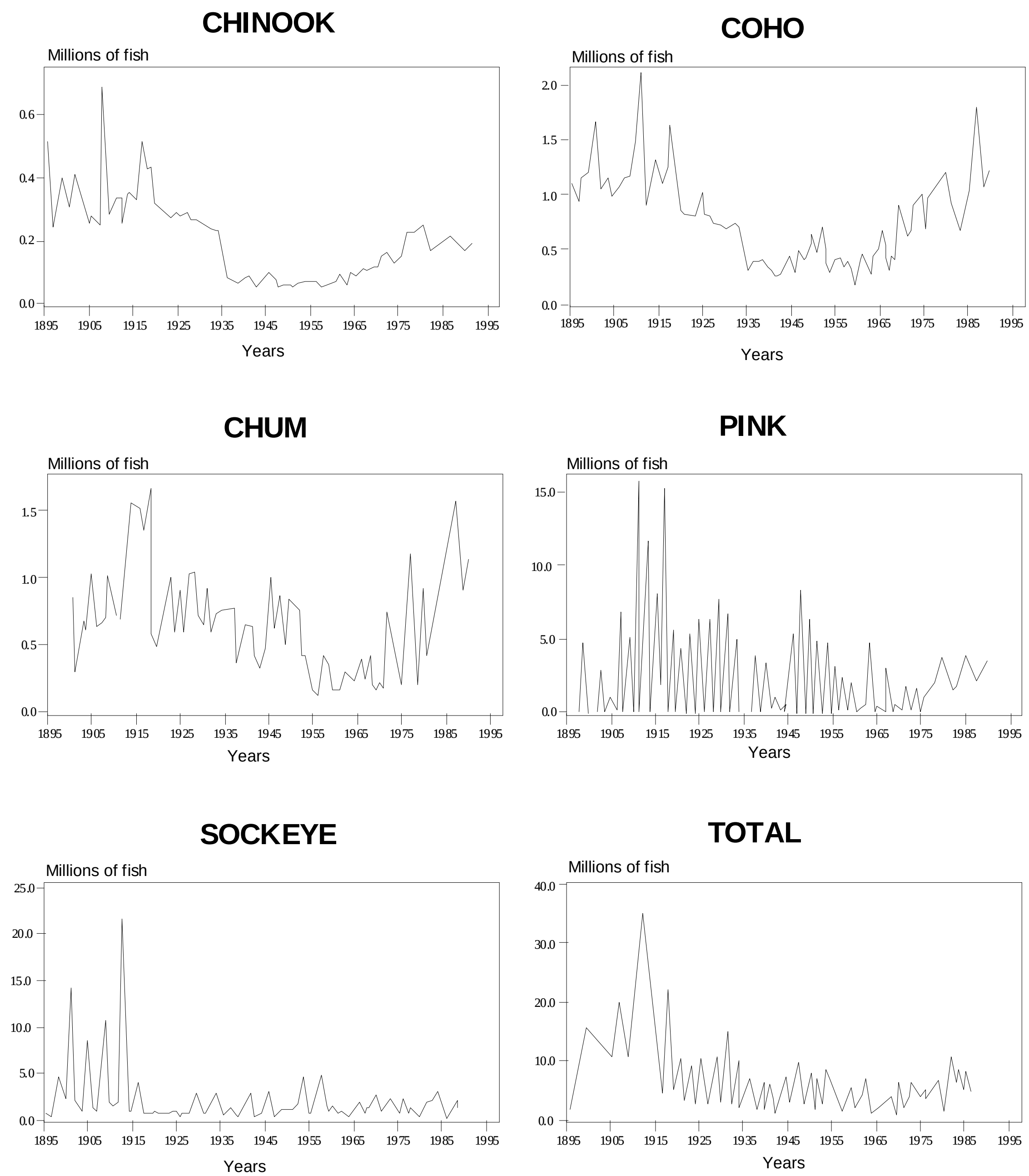


Figure 10. Estimated and reported total catch, in numbers, of Puget Sound salmon from 1890's to 1990's [390, 57a, 538b].

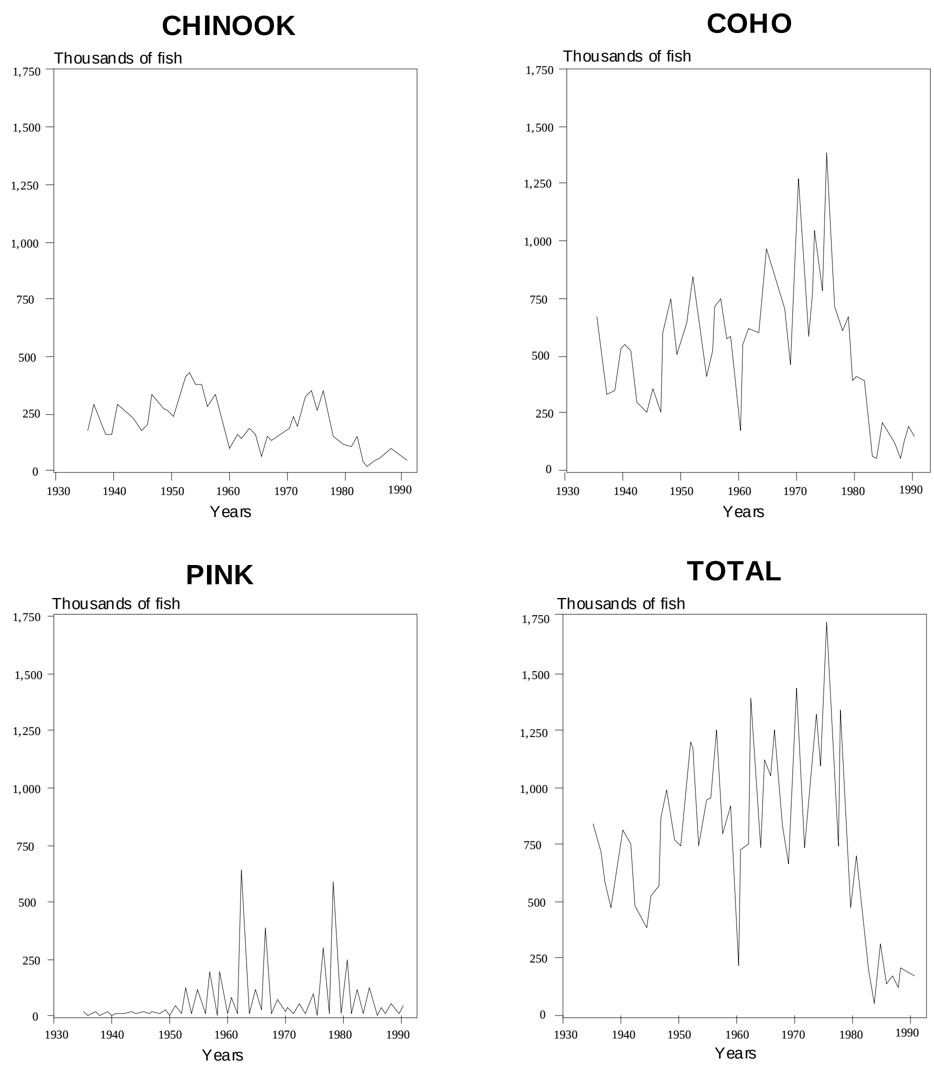


Figure 11. Washington total ocean commercial troll catch, in numbers, of salmon from 1930's to 1990's [390, 538b, 388a].

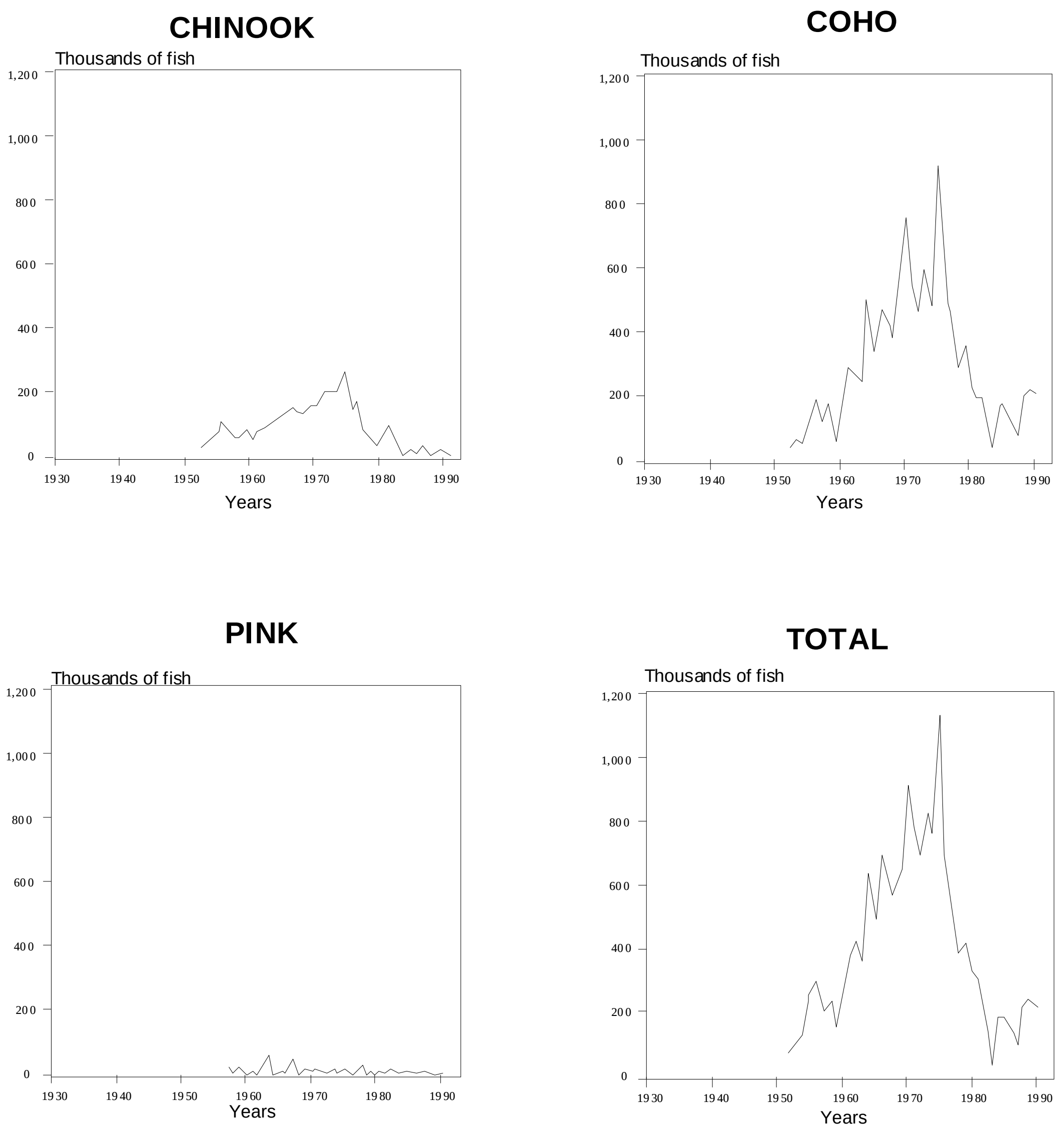


Figure 12. Washington ocean sport catch, in numbers, of salmon from 1950's to 1990's [390, 538b, 388a].

The salmon species complexes in the Columbia River, Puget Sound, and Coastal Washington and Oregon, except for Puget Sound chum, have never recovered to the numbers that existed when commercial harvest was initiated. Increased hatchery production did enhance some fisheries, notably the rise of the coho salmon runs in the 1960s, and chum salmon runs in Puget Sound. In general, however, artificial propagation has failed to rebuild the runs to former levels [394], and in some instances likely contributed to the further decline of wild stocks [209]. Hatchery production has also contributed to the harvest of wild salmon by creating socioeconomic incentives that maintain mixed-stock fisheries.

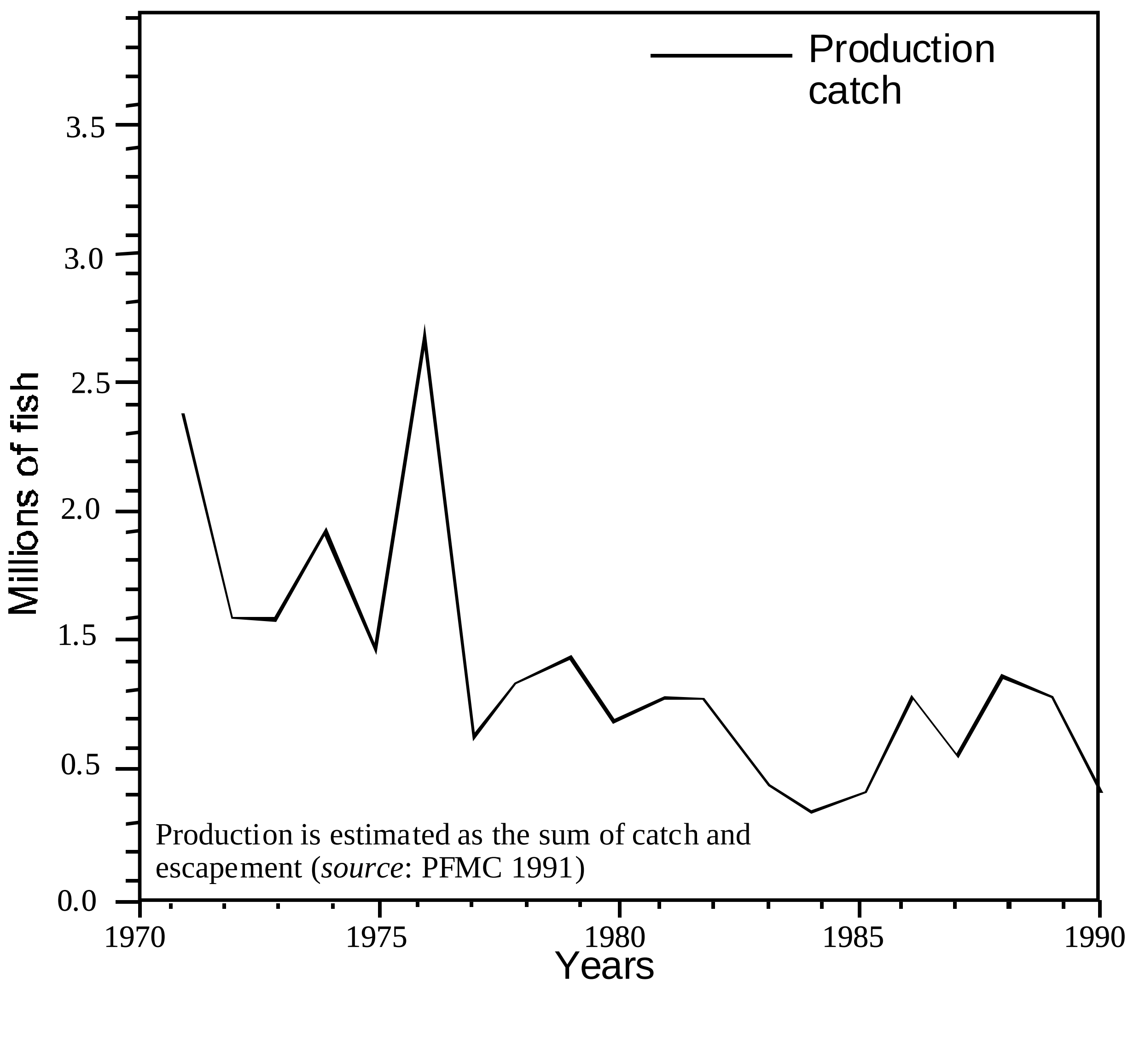


Figure 13. Estimates of Oregon coastal coho salmon production and harvest from 1970's to 1990's [387b, 388a].

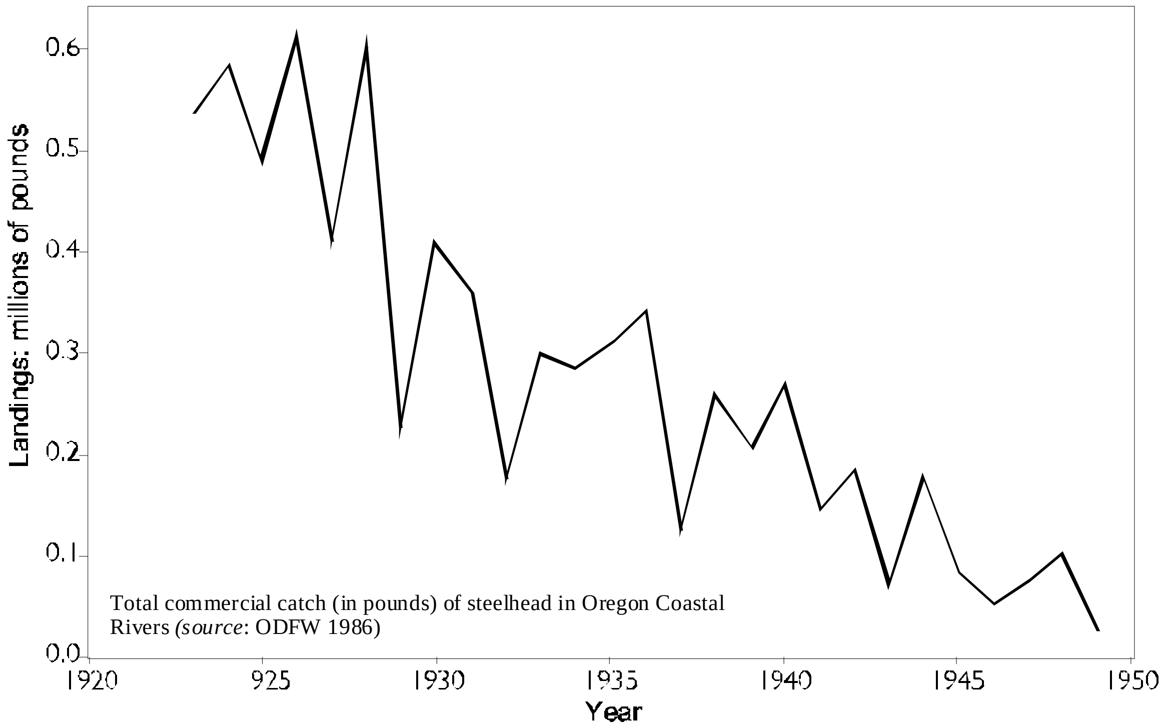


Figure 14. Total commercial catch, in pounds, of steelhead in Oregon coastal streams from 1920's to 1940's [387a].

Admittedly, managing salmon fisheries is a challenge, and past management approaches were generally commodity/extraction-based; however, this approach has significantly contributed to the decline of wild stocks [544]. Wild salmon life history characteristics that contribute to this challenge include wide geographic distribution with extensive feeding and spawning migrations; complexity of life history forms, ages, and sizes; and the death of most adult fish after spawning only once. Fishing activities that contribute to the problem include: indirect mortality due to catch and release of undersized fish (by-catch), out-of-state domestic and foreign interception, conflicts among user groups, and the mixed-stock fisheries.

A major dilemma that fishery resource agencies find themselves in is how to selectively harvest hatchery salmon, while still meeting spawning escapement goals of wild stocks of salmon. Hatchery-produced salmon co-mingle with wild salmon in ocean waters, and as a result, a mixed-stock fishery is created. If harvests are allowed in such mixed-stock fisheries, then wild and hatchery fish will be caught at rates that only hatchery fish can sustain. Wild salmon cannot withstand the high hatchery exploitation rate because they are exposed to a full range of natural and human-caused selection pressures and mortalities. Hatchery fish are sheltered from mortality factors that normally occur during incubation and freshwater rearing. At smolt migration, many more progeny are still alive per hatchery female than per wild female. Thus, hatchery populations can maintain smolt output at a consistent level with far fewer spawning adult fish than can wild populations. This condition enables hatchery stocks to withstand higher rates of harvest than wild stocks; however, even hatchery stocks eventually succumb to the high exploitation rates through changes to smaller adult size [517], or different time of return [190]. Therefore, high fishing exploitation rates are associated with fishery resource management agency policies, and agency policies also determine hatchery policies and practices. The current demand by certain interests to protect wild stocks can be in direct conflict with the agency mandate to enhance or supplement current stocks with hatchery-produced fish to ensure sustainable harvest for the major user groups. This conflict will have an important bearing on future management of salmon fisheries and hatchery practices. Live capture selective fishing, including live release of wild unmarked fish and retention of marked hatchery fish, is potentially an option [279].

Spawning Escapement Goals

Spawning escapement goals (the number spawners required to perpetuate the population [254]) are set by fishery managers to determine the portion of the estimated returning adult population that can be harvested. Recently Knudsen [254] reviewed the methods used along the west coast to establish wild salmon escapement goals, and found that of 854 management units 8 (1%) were set by methods that were rated excellent (i.e., using methods that combined information in a way that most effectively characterized the management unit's production potential), 142 (16%) were rated as good, 499 (58%) were rated as fair, 13 (2%) were rated as poor, and 192 (22%) had no goals established at all. Analysis of annual spawning escapement data by Konkel and McIntyre [257], collected for naturally spawning salmon populations in the Pacific Northwest between 1969 and 1984, suggests that escapements are down for coho and chum; but up for chinook, sockeye, and pink salmon. In general, escapement trends have been downward since 1970 for all populations, even for those that have achieved their annual escapement goals.

According to the Pacific Fisheries Management Council (PFMC) [388] the state of Washington has established annual escapement goals for coho, chum, and chinook salmon and steelhead, and include wild and hatchery fish. Some escapement goals exist for pink and sockeye salmon that are mostly for wild fish. No determination has been made of the spawning escapement needs of sea-run cutthroat trout.   Spawning escapement goals have been established for 98 wild salmon stocks in Washington [538a]. These stocks include 30 coho salmon, 29 chum salmon, 27 chinook salmon, 9 pink salmon, and 3 sockeye salmon populations. Fifteen wild stocks of Washington steelhead have established annual spawning escapement goals [106]. Overall, for 113 wild salmon stocks in Washington with established spawning escapement goals, only 46 (41%) met these goals as of the early 1990's [390]. Escapements may have improved for some stocks in recent years due to fishery restraints.

In Oregon, escapement goals have been established primarily for chinook and coho salmon and include wild and hatchery fish. No determination of the spawning escapement needs has been made for wild steelhead, chum salmon, pink salmon, or sea-run cutthroat. In the early 1990s, spawning escapement goals were met for only 1 of the 2 populations of wild anadromous salmon in Oregon [390], being met for coastal chinook, but not for coastal coho salmon. Escapements may have improved for some stocks in recent years, due to fishery restraints.

The result of heavy exploitation in the fishery, along with major habitat loss over the past century is that the loadings of marine derived nutrients have been vastly diminished throughout Washington and Oregon rivers. A recent analysis of historical salmon cannery records from west coast rivers by Gresh et al.[174a], indicates that the number of salmon now returning to Washington and Oregon rivers is only 3.3 percent of the historical biomass (132-228 million kg down to 5-7 million kg). These authors conclude that: "This nutrient deficit may be one indication of ecosystem failure that has contributed to the downward spiral of salmonid abundance and diversity in general, further diminishing the possibility of salmon population recovery to self-sustaining levels."

The critical factor that salmon harvest managers need to face is how to reduce the annual salmon harvest, and achieve stock-by-stock ecosystem-based spawning escapement goals. With the exception of carcass supplementation programs, there has not been a concerted effort to manage salmon populations for the benefits they provide to the recovery of listed wildlife species (e.g., grizzly bears) or to the broader ecological systems. Salmon spawning escapement goals should not only replace a stock of salmon with sufficient numbers of high quality recruits, but also meet the needs of the broader aquatic and terrestrial ecosystems that depend on salmon for nutrients and carbon influx [47, 48, 319, 92]. Salmon harvest managers could take a lesson from the worldwide conventions for herring harvest managers where ecosystem function has been explicitly recognized through "...a precautionary, conservative approach to fisheries management." [541a].

For a more thorough review of the magnitude and characteristics of Northwest Pacific Coast salmon fisheries and habitat issues, we recommend the following readings:

Cone, J., and S. Ridlington. 1996. The northwest salmon crisis - A documentary history. Oregon State University Press. Corvallis, OR. 374 pp.

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UNDERSTANDING SALMON RELATIONSHIPS

Salmon As A Key Linkage In Biodiversity And Productivity

Ecological processes have been so altered by human activities, especially in the more densely populated regions, that natural resource and environmental management will need to expand from current site and case-specific methods, to landscape and ecosystem scale approaches. The struggle to develop the tools required for these scales of management has only just begun [269, 460, 365, 305]. The documents: *From the Forest to the Sea* [295], *Forest Ecosystem Management: An Ecological, Economic, and Social Assessment* [151], *Pacific Salmon and Their Ecosystems* [499], *An Ecosystem Approach to Salmonid Conservation* [485], *Fish Habitat Rehabilitation Procedures* [477] and *River Ecology and Management - Lessons From Pacific Coastal Ecoregion* [362] are recommended readings that describe the understanding of natural systems and processes and take a holistic approach to rehabilitation and restoration of watersheds and Pacific Nothwest ecosystems.

Anadromous salmon play an important role in maintaining an ecosystem's productivity. The seasonal migrations of millions of salmon between Pacific rim streams and the subarctic Pacific

Plate #19. Chum salmon carcasses in Kennedy Creek, Washington. (Photo by: Jeff Cederholm).

Ocean appear to increase overall terrestrial productivity. Key processes discussed here are the transport of materials, energy and nutrients between marine, aquatic, and terrestrial ecosystems with emphasis on salmon as a transport vector. From a broad ecosystem management perspective, the status of salmon metapopulations is a powerful indicator of human adaptation to boreal biomes [348, 464, 419]. Sibatani [464] has suggested that salmon are the "canary in the mineshaft"; the mineshaft in this instance being entire subarctic ocean basin ecosystems. Cederholm et al. [92] review and discuss the mechanisms of salmon nutrient transport and the significance to terrestrial and freshwater ecosystems. The following discussion suggests a need to understand and apply information on the exchange of materials, energy, and nutrients, between the aquatic and terrestrial ecosystems of the northern Pacific Basin. Such an application would occur at multiple geographic and temporal scales, examining both healthy and depressed salmon populations under varying conditions. Effectively applied, managers would be able to define and achieve long-term ecosystem management success not just for salmon, but for numerous other fish and wildlife resources and the overall health of the environment.

Biomass of Salmon Runs As An Energy Source
Organic matter that supports the trophic system of fresh water ecosystems is provided from both autochthonous and allochthonous sources. Common types of autochthonous sources are: algae, mosses, vascular plants, and phytoplankton. All of these factors are found in freshwater, and generate organic matter through the process of photosynthesis. Common types of allochthonous input include leaves, needles, wood and insects from the terrestrial environment and dissolved organic matter carried in groundwater that enters the water body. Salmon provide an important source of allochthonous organic matter for Pacific Northwest fresh water ecosystems [248, 47, 239]. Salmon spawning runs transport organic matter and nutrients from the northern Pacific Ocean to their natal spawning grounds. The organic matter and nutrients carried in the biomass of the salmon runs is input to the trophic system through multiple levels and pathways including direct consumption, excretion, decomposition, and primary production. Direct consumption may occur in the form of predation, parasitism, or scavenging on the live spawner, carcass, egg or fry life stages. Carcass decomposition and the particulate and dissolved organic matter released by spawning fish (e.g., eggs and milt, excrement) delivers nutrients to primary producers. Potential nutrient or energy pathways and factors influencing biomass cycling of spawning salmon is graphically depicted in Figure 15.

Freshwater and estuarine ecosystem productivity depends upon nutrient inputs and retention. Larkin and Slaney [266] and Munn et. al. [339] discuss nutrient cycling and the nutrient spiraling concept, whereby nutrients spiraling downstream can influence aquatic system functions for considerable distances. Larkin and Slaney [266] and Munn et. al. [339] also discuss the importance of instream habitat complexity (wood debris complexes) for increasing productivity by increasing salmon carcass retention; citing Cederholm and Peterson [90] and Cederholm et. al. [91]. Retention of nutrients also occurs at smaller scales and through chemical and physical processes. Organic molecules in water are rapidly absorbed onto the biofilm that covers most aquatics surfaces [47]. Transport of salmonid organic matter and nutrients across mosiacs of inchannel, riparian, floodplain, and estuarine habitats in a watershed may then occur as water, sediments, and organic debris are redistributed; as in freshets. The discussion that follows emphasizes the necessity of retention mechanisms and how the physical and biological complexity of the aquatic, riparian, and wetland zones enhances this function.

Sportsmen and naturalists have long recognized the importance of salmon runs to the natural economy of streams, as this quotation by Haig-Brown [180] reveals:

> *"The death of a salmon is a strange and wonderful thing, a great gesture of abundance. Yet the dying salmon are not wasted. A whole natural economy is built on their bodies. Bald eagles wait in the trees, bears hunt in the shallows and along the banks, mink and marten and coons come nightly to the feast. All through the winter mallards and mergansers feed in the eddies, and in freshet time, the herring gulls come in to plunge down on the swifter water and pick up the rotting drift. Caddis larvae and other carnivorous insects crawl over the carcasses that are caught in the bottoms of the pools or against the rocks in the eddies. The stream builds its fertility on this death and readies itself to support a new generation of salmon."*

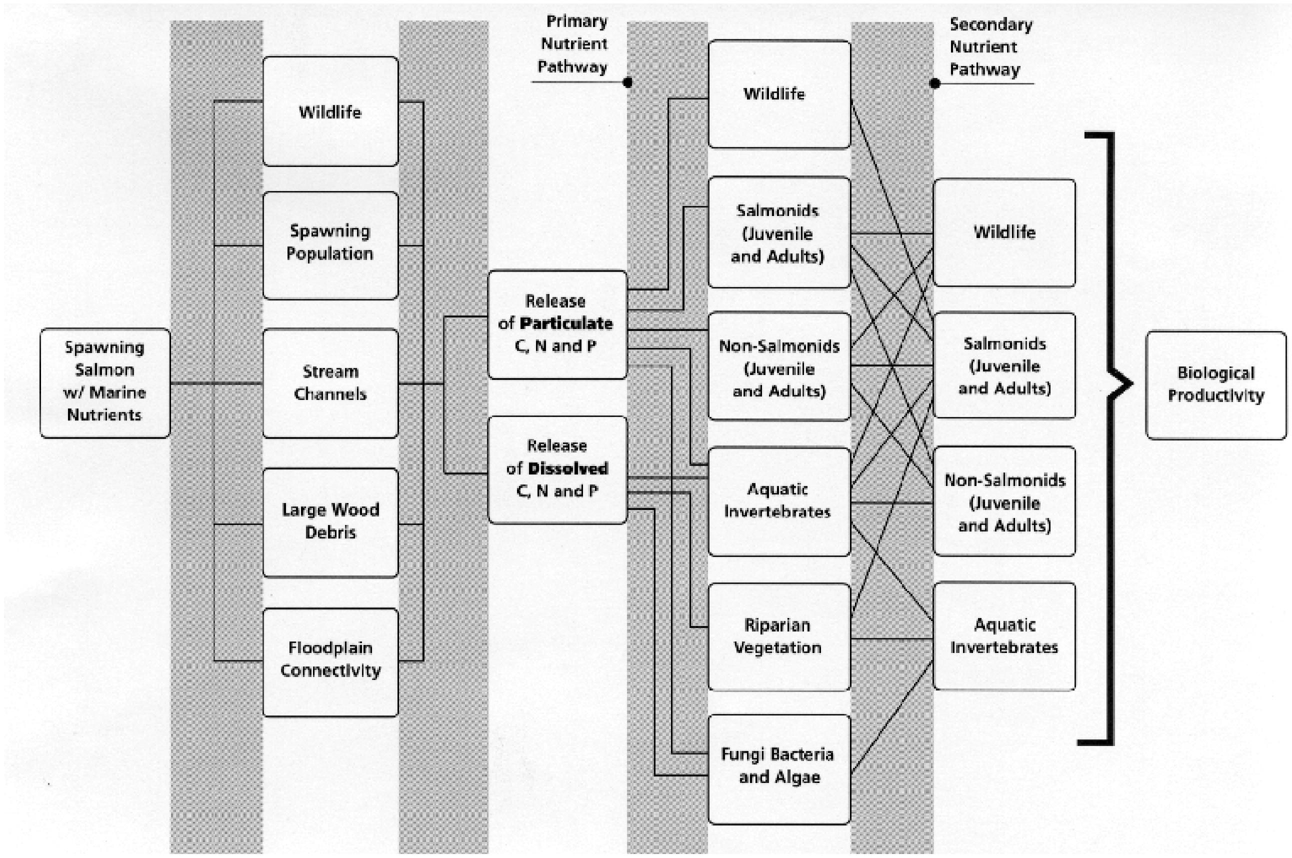

Figure 15. Factors of stream complexity and marine derived nutrient pathways that influence biological activity [92].

The scientific community has also recognized the contribution of nutrients and organic matter from spawning salmon for some time. Juday et al. [241] estimated that sockeye salmon transported in excess of 2 million kg of organic matter and 5000 kg of phosphorus to the Karluk River system in Alaska in an average year. This recognition resulted in sockeye lake fertilization programs in British Columbia and Alaska, to replenish lost nutrients caused by fish harvest [497, 496]. Over the last 10 years stable isotope analysis has enabled direct measurement of marine-derived nutrients in stream [248, 47, 239] and lake [249] ecosystems. These studies have firmly established the need to consider the importance of salmon biomass as a flow of energy and nutrients into the freshwater and estuarine food webs of the Pacific Northwest.

Nutrient levels in fresh water and estuarine systems can be substantially enriched by the organic inputs of spawning runs. The majority of material transported to freshwater by some species of anadromous salmon is of marine origin. Mathisen et al. [298] demonstrated that over 95% of the body mass of some salmon species is produced during ocean residence; the remainder represents mass accumulated in freshwater prior to migration to the sea. The species of salmon that spawn at high densities (e.g., chum, pink, sockeye) significantly alter nutrient loadings and budgets in the freshwater systems where they spawn. In Kamchatka, Krokhin [262] reported that 35-40% of the yearly total phosphorus input to a lake was transported by spawning sockeye salmon, as was much of the nitrogen input to the system. Similar results have been reported for the Iliamna Lake system in Alaska [122, 297, 298, 249] and for the Paratunka River basin, Kamchatka [261, 262]. Nutrients from spawning pink and chum salmon have been shown to not only enrich the freshwater and estuarine habitats where they spawn, but also the estuarine habitats downstream [62, 503]. Munn et. al.[339] consider changes in nutrient loading and cycling and ecosystem productivity that could result from restoration of historic salmonid populations to the Elwha River system in Washington state. The study indicates a potential 65-fold increase in nitrogen and phosphorus loadings from salmon returns. They conclude that restoration of the Elwha River system salmon runs would have a profound effect on the primary and secondary production in the system.

Table 7 shows calculations of the annual input of organic matter, nitrogen and phosphorus to freshwater catchments within the Puget Sound Basin of Washington, resulting from recent peak spawning escapement levels. These overall inputs of 189 metric tons (mt) of nitrogen and 22 mt of phosphorus equate to approximately 1.9 and 1.2 percent, respectively, for the 10,000 mt and 1,909 mt recent annual outputs of nitrogen and phosphorus from freshwater as calculated by Inkpen and Embrey [226]. While the percentages in the table indicate that current salmon escapements are generally a minor source of nitrogen and phosphorus to freshwater habitats within the basin, further examination of information on nutrient loading sources, including salmon runs, indicates that pre-commercial exploitation era escapements were a significant component of the nutrient budgets for the freshwater habitats accessible to anadromous salmon.

Available data on calculated present nutrient loading and projected salmon return loads for a restored Elwha River system were used in comparison with the above values for Puget Sound to illustrate the likely order of magnitude of the difference between the pre-European settlement inputs and present conditions. Annual nutrient inputs of 29.8 mt of nitrogen and 3.5 mt of phosphorus are projected for a 980 mt biomass of restored salmon returns based on Munn et. al.[339]. The nutrient levels are approximately 40% and 13%, respectively, of the present 74.5 mt of nitrogen and 27.3 mt of phosphorus loads to the Elwha watershed [226]. The Elwha River ratios of salmon origin nutrients to total nutrients are respectively 21 and 11 times the percentages of 1.9 and 1.2 for Puget Sound. This is in part due to human induced enrichment of some Puget Sound systems from agricultural and urban land uses several times those in the relatively undisturbed Elwha River system. These preliminary estimates as to the levels of nutrient loadings to the water column and sediments, while crude, should be sufficient cause to trigger some rethinking of what constitutes healthy baseline water and sediment quality for Puget Sound and Pacific Coast streams and estuaries.

Productivity of freshwater ecosystems may be substantially affected by the nutrient and organic matter contributions of spawning salmon. In Lake Dalnee, Kamchatka, chronically low returns of sockeye salmon over a period of several years brought about: (1) a decrease in annual primary production of 20 percent; (2) a 30 percent decrease in total annual production of zooplankton; and (3) a decrease in total annual production of plankton-eating fish (including juvenile sockeye) of 45 percent [262]. The number of returning sockeye salmon can alter the productivity of lake ecosystems [241, 297, 249]. Richey et al. [425] found that kokanee salmon (O. nerka) carcasses added 44.6 kg of phosphorus to a small tributary of Lake Tahoe, California, raising the phosphate concentration of the water by 4-6 µg/L. Algal productivity was stimulated as a result of the increased availability of nutrients.
Even low spawning densities can provide significant contributions of nutrients to the system. Juvenile coho, steelhead and cutthroat in a small stream in western Washington obtained from 25% to 40% of their N and

C from dead coho salmon that spawned in the stream [47]. Aquatic insects also contained high levels of marine-derived N and C, and the foliage of plants growing along the streams also contained nitrogen of marine origin [47]. The direct feeding of salmon fry on salmon carcasses has been known for a long time in the Amur River of Asia [377], however, the growth benefits for juvenile salmon has only recently been documented in North America [47].

able 7. A first order approximation of body biomass and nitrogen and phosphorus imports in metric tons (mt) to the freshwater catchments within the Puget Sound Basin resulting from ecent peak wild spawning salmon escapements.

atershed			**Species**					
Unit Name	Chinook	Chum	Coho	Pink	Sockeye	Totals	Nitrogen	Phosphorus
Nooksack	0	334	20	294	0	648	19.7	2.3
amish	0	25	35	n/a	n/a	60	1.8	0.2
NS Independents	0	0	0	0	0	0	0.0	0.0
Skagit	127	797	26	214	0	1,164	35.4	4.2
tillaguamish	8	453	13	38	0	512	15.6	1.8
Snohomish	36	413	53	150	0	651	19.8	2.3
Lake Washington	48	0	0	0	215	263	8.0	0.9
Duwaumish/Green	74	8	2	0	0	85	2.6	0.3
Puyallup	0	8	19	3	0	30	0.9	0.1
Nisqually	16	349	2	1	0	367	11.2	1.3
South Sound	190	1,345	6	0	0	1,541	46.8	5.5
Hood Canal	27	791	3	13	0	834	25.3	3.0
trait of Juan de Fuca	42	24	2	4	0	73	2.2	0.3
Totals	567	4,548	180	717	215	6,227	189.3	22.4

The loadings in metric tons were derived by multiplying recent escapements for each species by orresponding average weights and body composition proportions for nitrogen and phosphorous. Escapement data are from Washington Department of Fisheries, Washington Department of Wildlife, and Western Washington Treaty Indian Tribes [542, 539]. Average sizes of almon by species are from Ricker [426] as quoted in Larkin and Slaney [266]. Proportions of body omposition for nitrogen and phosphorous are from Larkin and Slaney [266]. This table is a urthering of the concepts discussed in Lichatowich [277]. This is an initial approximation of utrient imports, more complete data may be available from multiple fish management agencies i.e., Washington Department of Fish and Wildlife, Western Washington Treaty Indian Tribes, Oregon Department of Fish and Wildlife, etc.).

Nitrogen and carbon contained in the nonanadromous rainbow trout residing in a southeast Alaska stream was derived almost entirely from the large numbers of pink salmon which spawned at the site [248]. Growth rate, condition factor and population density of juvenile coho and steelhead increased dramatically after addition of coho salmon carcasses to two small streams in southwestern Washington [48]. Additional work by Michael [318] and Adams [1] indicate that juvenile coho spawned in year N reap the benefits provided by all species of salmon spawning in year N+1. Johnston et al. [239] found a relationship between the proportion of marine-derived nitrogen in insects and the density of spawning sockeye salmon in tributaries of the Stuart River in interior British Columbia. Therefore, the productivity of freshwater habitats may be influenced by the abundance of spawning fish using the system. Also Shuldt and Hershey [462] showed direct effects of salmon carcasses decomposition on elevating periphyton accrual and dissolved nutrients in Lake Superior tributaries.

Macroinvertebrate communities in streams receiving salmon runs can change in response to spawning activity and nutrient enrichment. In a Snoqualmie River, WA tributary and in Kennedy Creek, Washington, Minakawa [324] found the presence of salmon carcasses and eggs produced a two-fold or greater increase in total insect densities and biomass compared to control reaches. Piorkowski [404] found insect taxa richness and diversity to increase in response to nutrient enrichment from salmon carcasses in southeast Alaska, and suggested that insect colonization of carcasses facilitated decomposition and subsequent nutrient release. Bilby et al. [47] found all functional feeding groups except insect shredders to be enriched with marine origin isotopes of nitrogen and carbon in western Washington streams after coho salmon spawning. Some aquatic invertebrates such as stoneflies (Plecoptera: Alloperla) [375] and Dipteran flies (Chironomidae) [131] will scavenge for dead salmon eggs and alevins within the gravel. Limnephilid caddisfly larvae are attracted to recently expired salmon and have been observed feeding directly on fish flesh [404, 324].

Terrestrial insects including fly maggots (Diptera) have also been observed feeding heavily on salmon carcasses in streams in the Queen Charlotte Islands of British Columbia [422], but generally little work has been done to systematically document these activities. Maggot larvae have commonly been observed consuming beached salmon carcasses during the warmer months of the spawning season along the spawning reaches of several Washington streams. Dead chum salmon along Kennedy Creek in South Puget Sound often have their heads filled with maggots (Cederholm, personnal observation). Chinook carcasses along Puget Sound Basin rivers can be reduced to skeletal remains by maggots within a two week period; fall freshets frequently have been observed to wash the carcasses and masses of larvae back into the stream where they are then available as food for juvenile salmon and other organisms (Graeber, personal observation). Hornets have also been observed to feed on carcass remains during warm fall weather periods in the same areas; they are especially attracted to exposed fresh flesh or blood (Graeber, personal observation).

Quantitative measurements of salmon carcass consumption in the terrestrial environment has focused on their utilization by high profile species like Bald eagles along the Skagit River, Washington [490, 187] and grizzly bears along the Columbia River [205]. But Cederholm et al. [91] recorded 43 taxa of mammals and birds present on small Olympic Peninsula streams at a time when coho salmon carcasses were present, and found that 51% of those taxa had fed on carcasses. Skagen et al. [475] in their study of human disturbance on an avian scavenging guild, observed significant bird scavenging of chum and coho salmon carcasses along the North Fork of the Nooksack River, Washington. The primary bird scavengers were eagles, crows, and glaucous-winged gulls. Additional information on observations of wildlife predation and scavenging on salmon is presented in Appendix VII.

Plate #20. Fly maggots eating a chum salmon carcass at Kennedy Creek, Washington. (Photo by: Jeff Cederholm).

Cederholm et al.[91] also reported that black bears, raccoons, and river otters increase food availability for terrestrial species incapable of removing carcasses from the stream. The larger animals rarely completely consumed the carcasses they removed from the stream, and were often followed by an array of other smaller birds and animals who fed on the "leavings". A similar interaction occurred at McDonald Creek, Glacier National Park, Montana, where kokanee salmon captured by grizzly bears were incompletely consumed, leaving remains for birds and small mammals[486].

As the above studies indicate, spawning salmon provide a source of carbon, nitrogen and phosphorus essential to maintaining the production of salmon juveniles and other trophic levels of the stream. Accumulating evidence suggests that spawning salmon populations are an important link to the adjacent riparian and terrestrial communities, and indeed, fortifies the role of salmon as a keystone species, wherein the integrity and persistence of the entire community is contingent upon the population's actions and abundance[559].

Pacific Salmon Provide Key Ecological Functions

The key ecological functions that spawning salmon play within certain freshwater ecosystems may be illustrated with a well-documented case study from McDonald Creek in Glacier National Park, Montana. This stream is a principal spawning tributary for the Flathead Lake/Flathead River ecosystem. The triggering event in the series of changes that cascaded through this ecosystem was caused by the introduction of an exotic species, the opossum shrimp *(Mysis relicta)*, from 1968 and 1975[486]. The shrimp were added to the lake as a food source for kokanee salmon, but behavioral patterns made them unavailable for consumption. Opossum shrimp are voracious predators of zooplankton, the principal food of the kokanee. The shrimp decimated the zooplankton in the lake and by the late 1980s the lake and McDonald Creek spawning kokanee population had collapsed. These fish served as an important food source for various birds and mammals that had fed upon them in the spawning tributaries. One of the most prominent predator and scavenger utilizing this resource were bald eagles that gathered by the hundreds during the kokanee spawning period. In 1981, spawning kokanee in excess of 100,000, attracted 639 eagles, the densest eagle concentration south of Canada. Beginning in 1987 eagle numbers declined along with the kokanee, reaching a low of just 25 birds in 1989. It is feared that loss of the kokanee spawning run could lead to higher eagle mortality during migration or during winter unless the birds can find alternate food resources, a prospect that is not likely in that ecosystem [486]. A number of other bird and mammal species that used the McDonald Creek kokanee also have been displaced [486]. Gulls, mergansers and mallards commonly fed on kokanee carcasses, while Barrows and common goldeneyes and dippers fed on loose eggs. Mammals that fed on spawning kokanee or carcasses along McDonald Creek, including grizzly bears, coyotes, mink, and river otters, are now less common along the creek.

Estuaries, where rivers and streams meet tidal influence and enter the ocean, act as traps for sediments, organic materials, and nutrients washed from watersheds. Some species of Pacific salmon typically spawn near saltwater or even beginning within the upper reaches of estuaries and often spawn at very high densities. The effect of salmon carcasses on the nutrient dynamics and trophic productivity of estuarine systems is just beginning to be examined. Kline et al. [248] reported that approximately 30,000 pink salmon spawned within 1.2 km of the estuary of Sashin Creek in southeast Alaska. In southwestern Washington, the 5 km of Kennedy Creek accessible to anadromous fishes has supported as many as 80,000 spawning chum salmon (WDFW unpub. data). Using the size and body composition information previously cited (under the Elwha River discussion), we estimate that this peak escapement to Kennedy Creek delivered approximately 398 mt of salmon flesh containing 12 mt of nitrogen and 1.4 mt of phosphorus to 0.075 km^2 of stream channel area (5 km with an average channel width of 15 m). The nutrient loading per unit of channel area would be 160 mt/km^2 nitrogen and 18.7 mt/km^2 phosphorus. The salmon carcass materials, or their nutrients, in dissolved phase or sorbed to sediment particles may be carried to the estuary through various physical, biological, and chemical processes [47, 266, 339]. Therefore, a nutrient link may function between adult salmon carcasses and juvenile salmon rearing in the estuary. For example, Fujiwara and Highsmith [159] found elevated stable isotope ratios of nitrogen in *Ulva* sp., an estuarine macroalga, following the decomposition of salmon carcasses in Seldovia Bay, Alaska. *Ulva* sp. are a major food source for harpacticoid copepods, which in turn are a preferred prey of juvenile chum salmon fry in the estuary. Thus, the contribution of nutrients and organic matter from salmon carcasses may be a substantial source in some systems and may be a key factor in promoting estuarine productivity. The importance of estuaries as nursery zones for anadromous salmon along the Pacific Northwest coast is well documented [196, 355, 289, 397, 454, 194], the role carcasses play in maintaining productivity of these systems may be critical in supporting the health of salmon populations [159].

The role salmon populations play as a key vector in the recycling of energy and nutrients inland from the North Pacific Ocean to aquatic and terrestrial ecosystems is now gaining recognition as a critical component of ecosystem function [350, 348, 463, 464]. River and lake fertilization with inorganic nutrients has been undertaken with ecosystem restoration in mind in some British Columbia systems [476, 496, 16, 15], however, artificially supplementing inorganic nutrients may not fully mitigate for the loss of the multiple pathway flow of energy and materials provided by naturally spawning salmon.

Salmon As Vectors In Broader Nutrient Cycling

The flux of nutrients is essential for the continuity and stability of any living system [412], and nutrients provide a link between aquatic and terrestrial ecosystems [61, 317]. Biological vectors through which materials and energy are transported include migration of animals (i.e., mammals, birds, fish) that carry nutrients across ecosystem boundaries [61, 379, 463, 464, 349]. Therefore, the role and importance of salmon in the freshwater and terrestrial ecosystems can be recognized within the context of broader nutrient cycling, and spawning migrations of salmon represent an obvious example of this process. Other means of moving nutrients upstream, such as the emergence of the adult stages of insects and meteorological vectors, are considered to be relatively insignificant compared to anadromous fish [278]. The nutrient-subsidy contributed by salmon in the North Pacific could potentially serve as a model for a more general, and global, aspect of nutrient circulation. Such studies may be supplemented by an assessment of the extent to which migratory birds, which travel long distances between boreal/subboreal zones and temperate and/or tropical regions, contribute to similar effects.

Using the discipline known as *Resource Physics*, Tsuchida [524] has explained how the hydrologic cycle and the convection of air are able to keep the earth in a low-entropy state [see also 350]. The hydrologic cycle is in turn driven by solar thermal energy and the earth's gravity. Subsequently, inorganic salts (especially nitrates and phosphates), which are essential to formation and activities of animals, plants, and microorganisms, are eventually washed downstream [525]. Ultimately, these salts are dissolved in river water and transported to the ocean, where they attain the highest and most uniform concentration below the depth of 1,000 m, largely free from biological consumption in the absence of photosynthesis. However, due in part to ocean currents (local upwelling), these nutrients eventually find their way back to the surface waters. This occurs in northern temperate or subpolar oceans by the effective vertical mixing of seawater due to the approximation of water temperature between deep and shallow water, primarily during colder seasons. Finally, uptake of these salts by marine plants near the surface, where photosynthesis is possible during the warmer seasons, allows a means through which other animals are able to derive and transport the nutrients inland. For example, Tsuchida [525] speculates that in coastal regions, some birds will carry nutrients back to the land after deriving them from the consumption of marine organisms. Bird excrement is a fertilizer rich in inorganic matter, especially phosphates, as evidenced by the material deposits (Peruvian bird guano) on tropical sea islands. Sibatani [463, 464] points out that another, arguably more significant way that nutrients are transported back onto the land is by anadromous fish swimming up, spawning, and dying in the many rivers of the Asian and North American continents. Murota and Faculty of Environmental Studies [351] discussed how migratory fish move ocean nutrients inland and benefit the Siberian forest and its various wildlife inhabitants (Figure 16).

> *"In the Edo era, some people in Japan started to notice that forests along seashores or rivers attracted fish towards them. It was considered that a forest could give benefits to fish in the forms of shadow as shelter, nutrients, and so on. This consideration remained in the minds of people living near waterfronts or forests after the Meiji Restoration (1868). When the first forest act was introduced at the beginning of the twentieth century, it contained the article ordering the conservation of uo-tsuki-rin, which literally meant 'fish-attaching forest.' This article is still valid in the present-day forest act of Japan."* [348.]

With regard to this *uo-tsuki-rin*, Sibatani [463 cited in 348], the Japanese scientist raises an interesting question:

> *"He thinks that it may be the fish that helps forests to grow rather than forests providing fish with comfortable spaces. This hypothesis comes from his research on the forests in Maritime Territories of Eastern Siberia, specifically along the Ussuri River, a tributary of the Amur*

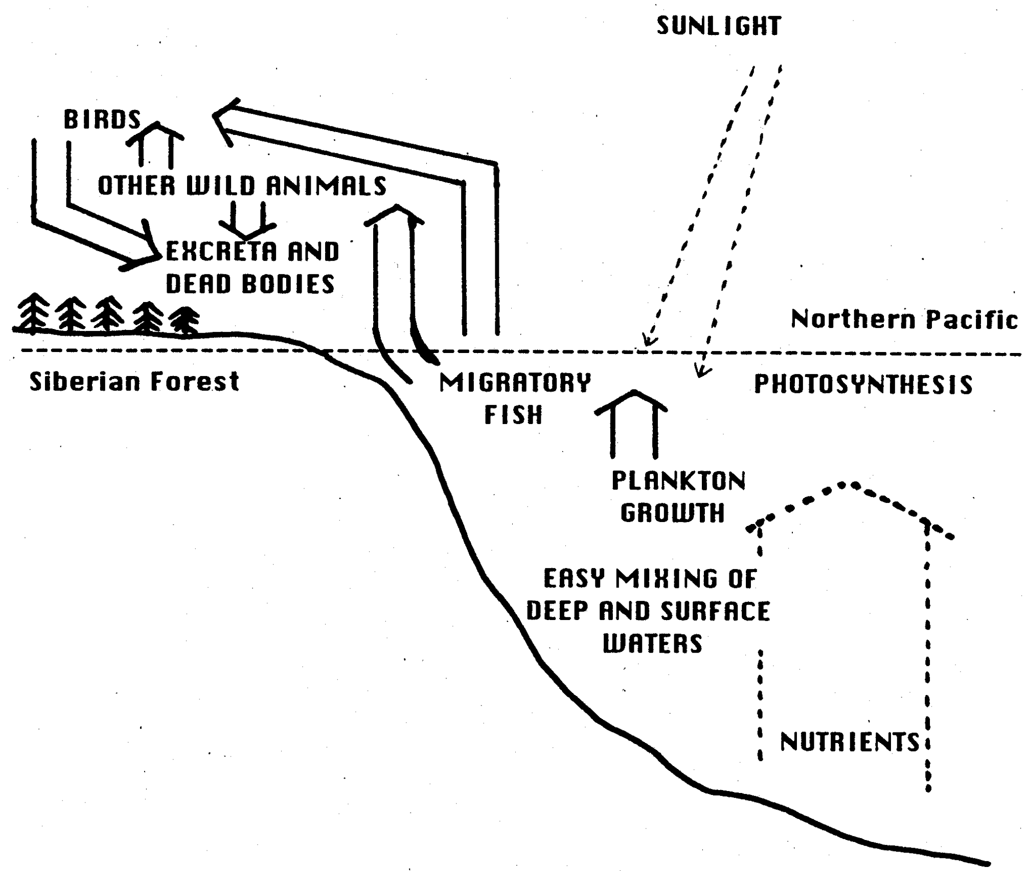

Figure 16. Andromous fish and the Siberian forest[351].

River. This area is subject to cold temperatures and receives very little sunshine, but there has been forest growth for a long period of time. Nutrients must have been carried from somewhere. But as there are no significant mountains in the upstream areas, the nutrients must have come from downstream, or more exactly, from the Northern Pacific, and the salmon as well as some other kinds of fish are likely to play a significant role as their carriers."

The theories of Sibatani [463, 464], Murota [348, 349], and Tsuchida [524, 525] cause one to reflect on the once bountiful salmon runs of the Columbia River. Before Europeans settled the Pacific Northwest, salmon and steelhead had access to over 20,000 km of main river and tributaries in the Columbia River basin [379]. The annual Columbia River salmon and steelhead run size was estimated to range between 8 and 16 million fish [379]. Using an average weight of 6.75 kg per salmon, spawning populations could have potentially contributed between 54 and 108 tons of nutrient annually. This amounts to between 2.70 and 5.40 tons per kilometer.

But what of the native people of the Columbia? Many traveled long distances to partake in the catch and consumption of salmon, and in doing so participated in the further cycling of nutrients over this vast watershed, and beyond. Some tribes of the upper Columbia were known to cross the Continental Divide to trade dried salmon for buffalo hides [379], thus providing an additional mechanism for transfer of marine-derived nutrients to the inland land mass. Salmon, wildlife, and humans, therefore, may be the most prominent carriers of ocean nutrients to inland ecosystems.

Salmon were, and are, a pervasive influence on the productivity of the otherwise generally oligotrophic ecosystems of coastal freshwater catchments of the Pacific Northwest region and the entire eastern Pacific rim. A coast wide estimate of the baseline biomass comparable to the above Columbia Basin estimate may also be useful to further discussions as to the scope of that influence. However, as noted above, run reconstruction is a problematic impediment. The peak historic commercial salmon cannery pack for the eastern Pacific rim are shown in Table 8 as a starting point. The cannery pack are a well documented, but very minimal, representation of baseline run size and biomass. The cannery pack tonnage can be readily expanded to round weight of the associated catch. The estimated catch tonnage shown in column 4 of Table 8 is derived by applying the 75% conversion factor for round to canned weight also reported by Cobb [99a]. A total run tonnage was then estimated by applying the Columbia River cannery pack to total run tonnage ratio (13,803:67,700; a run of almost 5 times the peak cannery pack), to each of the cannery pack figures (column 2) in Table 8. The resulting total run biomass in metric tons is presented in column 5 of Table 8. The coastal total run biomass estimate is 1.45 million metric tons. A more conservative expansion from cannery pack to total run tonnage is also provided in column 6, based upon a premise that northern areas may not have incurred as high a total exploitation rate. Column 6 (Table 8) uses an assumed 3:1 cannery pack to total run tonnage ratio. Given the fishery descriptions in Cobb [99a] and Crutchfield and Pontecorvo [110a], it appears reasonable that reported cannery pack catches in remote northern areas were a higher proportion of the total runs.

Maintaining the Salmon Link In Nutrient Cycling

As the decline of wild salmon continues throughout the Pacific Northwest [367], it is logical to assume that the productivity of some freshwater and terrestrial ecosystems will also decline. Decreased production could be self-perpetuating, as salmon stocks already in decline are likely to decrease further in a negative feedback loop [47, 266, 339]. The impending listing of many salmon stocks as endangered or threatened has forced federal and state government agencies to take aggressive action for salmon protection and recovery [366, 544].

There are numerous implications for fisheries management and the stream and riparian ecosystems that salmon inhabit. An obvious scenario includes allowing sufficient salmon to spawn in as many streams that were historically used by salmon as possible. A diversity of species that utilize several different stream orders will distribute marine nutrients throughout the entire watershed. Larkin and Slaney [266] have made a case for the need to consider nutrients loading levels and distribution in harvest management and hatchery production planning to sustain stream productivity for salmon. Munn et al.[339] have provided an estimate on the expected increase in nutrient levels and system productivity resulting from fully restored salmonid escapements under the proposed Elwha River restoration. Resource managers are beginning to consider the implications of changes in the flows of salmonid organic matter and nutrients may have on the levels of sustainable fish and wildlife management [339, 266].

Numerous implications for water quality management exist within the native range of the Pacific

Table 8. Peak Cannery Packs and Estimated Round Weight of Associated Catches and Estimated Total Run weights for all Species of Pacific Salmon in the Northwest and North America Prior to 1930.

Area	Peak Year	Cannery Pack		Round Weight of Pack	Estimated Total Run 5:1 ratio Expansion (Columbia Rv)	Estimated Total Run 3:1 ratio Expansion
		cases	metric tons	metric tons	metric tons	metric tons
Noyo River	1919	7500	164	205	807	305
Sacramento River	1882	200000	4364	5455	21513	8141
Eel River	1883	15000	327	409	1613	611
Klamath River	1912	18000	393	491	1936	733
Smith River	1925	7700	168	210	828	313
Coastal Oregon rivers	1911	138146	3014	3768	14859	5623
Columbia Basin	1895	629400	13732	17165	67700	25620
Willapa Harbor	1902	39492	862	1077	4248	1608
Grays Harbor	1911	75941	1657	2071	8168	3091
Coastal Washington Rivers	1915	31735	692	866	3414	1292
Puget Sound	1913	2583463	56366	70458	277884	105161
Fraser River	1901	998913	21794	27243	107446	40661
Outlying Districts	1928	1265522	27611	34514	136123	51514
Rivers Inlet	1925	197087	4300	5375	21199	8023
Skeena River	1922	482305	10523	13154	51878	19632
Nass River	1918	143908	3140	3925	15479	5858
Alaska	1926	6652882	145154	181442	715602	270809
Total		13486994	294262	367827	1450698	548996

Data on number of 48 pound cases of canned salmon packed and on 1.25 conversion to round weight are adapted from Cobb [99a].

salmon. The keystone role that salmon play in nutrient cycling needs to be recognized as an essential component to background water quality levels for healthy watersheds. The water quality regime of the high biodiversity of watershed communities supported by salmon runs may be very different than it is in other eco-regions. The energy and nutrient input pathways and timing for salmon runs are different than the energy and nutrient inputs from human activities. We will need to learn more about the range of historic nutrient loadings to freshwater and estuarine systems to understand how the declines in salmon runs and how disruptions to the sub-ecosystems of the salmon may be altering the biotic communities. From there we can better answer questions on appropriate allowable loadings and the water quality standards that will best sustain healthy communities.

In order to ensure nutrient cycles from the ocean back to the watersheds, the major vector of this process, wild anadromous salmon, must recover from their current status. Identifying and securing channels for the recycling of nutrients is an important component for maintaining biological diversity, at least in the Northern Pacific [463, 464, 348, 349]. The key to the sustainability of the human economy also may lie in these material cycles to some degree, as our economy relies heavily on healthy ecosystems to sustain the production of food and other resources [350, 349, 525]. The importance of the nutrient cycling link provided by anadromous salmon therefore illustrates the need for an uncompromising and all-encompassing plan to protect and recover wild salmon populations before the system is unrecoverable.

Plate #21. Jeff Cederholm holding a chum salmon at Kennedy Creek. (Photographer unknown).

WITH AN ECOSYSTEM PERSPECTIVE IN MIND - WHERE DO WE GO FROM HERE?

The need for an ecosystem approach to salmon management has inevitably grown in Washington and Oregon [365, 499, 305]. Terrestrial ecologists have recognized the influence human uses (and thereby disturbances) have had on terrestrial and aquatic ecosystems of large scales [295, 151, 545]. Some investigators have explored the significance of the salmon as a key ecological process vector on the broadest scales of energy and nutrient transport [559, 464, 348]. The use of salmon as an indicator of ecosystem health, or "the canary" is complicated by the fact that this canary is a food resource in high demand by humans [464].

The magnitude of the role of salmon populations as keystone vectors in energy and nutrient cycling inland from the Northern Pacific to freshwater and terrestrial ecosystems is now gaining recognition as a critical component to an overall understanding of ecosystem functions [464, 348, 349, 92]. Application of this knowledge to understand the cumulative impacts of human land use practices and fisheries exploitation on ecosystem functions is only just beginning. New tools are necessary to make management actions toward regaining lost productivity and biodiversity objectives [499, 305, 365].

Greater understanding of the hydrologic cycle has helped us to improve land and water uses to better adapt to our environment. Better understanding of geologic processes including the role of hydrogeology in shaping the landscape and controlling the rates at which sediments, and small and large organic debris cycle through watersheds is also leading to changes in views on land and water uses [434, 295]. Understanding nutrient cycling processes, pathways and the effects of nutrient loading has helped in managing water and sediment quality problems [435, 538, 245]. In much the same manner, an understanding of nutrient spiraling and cycling in streams [369] and the keystone role of anadromous salmon [266, 339] will be valuable, if not essential, to understand how we have affected coastal ecosystems and the processes that support them. Such an understanding will lead us to better identification of those management action options we may take to achieve desired future conditions.

Maser et al. [295] have added substantially to the literature on downstream and seaward movement of materials, energy and nutrient transport processes to and through aquatic systems. Their report compiled and presented a wealth of information on the inputs, fates, and effects of forest debris, particularly LWD, in freshwater, estuarine, and marine ecosystems. In essence, physical and chemical processes were well described, now the biological is considered. Adding estimates of the upstream flow of energy and nutrients via salmon to existing watershed processes literature, will provide a more complete picture of the large scale and long-term energy and nutrient cycles for entire watersheds. An understanding of the overall cycles and levels of productivity at this scale will provide the context for interpretation of local level trends in production and materials transport, utilization and storage. It has been well established that aquatic systems have metabolisms that function based upon physical processes, rates of loadings of materials, energy, and nutrients, rates of primary and secondary production, and resulting changes in standing stocks of fishes.

As a keystone species to the productivity and biodiversity of the ecosystems of the North Pacific basin, anadromous salmon closely link the management issues of the forests, the floodplains and lowlands, the estuaries and nearshore areas, and the ocean domains as a continuum. Materials, energy and nutrient budget analyses on an appropriate time scale will be necessary to estimate the potential effects that past land use practices have had on production and discern which ones persist. Budgets for the North Pacific Basin can theoretically be calculated in a similar manner to that already used on smaller systems. Then we can begin to use resulting information to provide a context for management decisions in various disciplines and forums that will affect materials, energy, and nutrient flows and stocks at various scales. To address the disconnects apparent in the current state of terrestrial and aquatic systems will require some estimate of many factors, including:

1. What is the status of the nutrient capital and rates of transport within the domains and the basin as a whole (nutrient budget)?
2. What is the range of the nutrient and materials capital and rates of transport (how does the current budget relate to the known ranges of standing stocks and rates of metabolism and transport)?
3. How have humans altered the nutrient budget?
4. What adaptive management actions might be warranted and feasible to push the terrestrial and aquatic systems toward the identified goals?
5. Are there some measures to employ in the interium until stocks of salmon can be restored?
6. What are the desired future conditions?

Early European settlement of the eastern North Pacific Rim territories provides many accounts of heavy extractions of forest resources [295, 276, 348, 464, 554, 110a, 70, 365]. Logging of the forests had the obvious effect of short circuiting the prior cycles that supplied woody debris to freshwater, estuarine, and marine ecosystems. In recent decades mechanized logging equipment combined with highly efficient ("clean") logging practices and slash burning to prevent wildfires and accelerate re-growth of planted conifers has further resulted in very little debris left on the site or entering streams. The store of vast quantities of nutrients in the form of the decayed woody debris and trapped detritus that serves as substrate for long-term nitrogen fixation and retention no longer exists. Large woody debris may continue to enter stream corridors, but not necessarily in the amount, size, and quality that it did in the past, thereby decreasing potential to provide stream structure and organic matter to food-webs [416, 299].

The long-term loss of the function of LWD as a primary component of the floodplain waterways, resulting from land and channel clearing, may well be more significant than the loss of the wood material itself. The resistance of the abundant woody material slowed the flows of water, sediment, and smaller debris; resulting in very complex valley floor stream-ways composed of multiple highly sinuous channels that were generally well connected to off-channel wetland systems by sloughs and high water channels. Put this liquidation of natural resource capital into the context of long-term climate cycles [189] and Maser et al.'s [295] long-term geologic and successional cycles, and one can begin to formulate management goals for ecological processes.

A combination of development activities have diverted water, shortened, straightened, cleared, dammed, diked, drained, filled and polluted the habitats of salmon. Early in settlement, logging and splash damming, land clearing for agriculture, and channel clearing for navigation appear to have had the most pronounced effects. The development and consumptive utilization of natural resources was highly dependent upon water-borne transportation and patterns of impacts are reflective of navigation-centered commerce. Continuing development for agriculture, industry, and urban growth has resulted in further losses through conversions to other uses. Impacts have become more pervasive throughout the landscape as transportation infrastructure and vehicle capabilities have increased. Releases of persistent toxins has contaminated coastal sediments. Thus available freshwater and estuarine salmon habitats also continue to be degraded by ongoing land uses [365, 295, 454, 174, 526, [554, 245].

Desired Future Condition

The inability of the various interest groups to resolve conflicting and agreed-to goals or conditions has been identified as the fatal gap in salmon management [365, 54]. Describing the desired future condition of the terrestrial and aquatic ecosystems and identifying and defining human actions can influence movement of ecosystems toward those conditions. The institutional changes suggested by Lichatowich [277] will be necessary to implement the long-term management approach required. Some of those institutions are known and have been in use during other eras where human land and resource uses appeared to have been indefinitely sustainable [464, 554].

In spite of the high potential commodity value of the harvest and our knowledge that the Pacific salmon is a key driver for the biodiversity and productivity of the northern Pacific basin, we have not developed the strategies for effective long-term management of the resource's health. The widespread use of salmon hatcheries has also significantly reduced the amount of salmon carcass nutrients available for the aquatic food webs. Modern human culture has not fully adapted to the environment of the northern Pacific Basin. The environment of our region is showing the signs of stress all around us which indicates the failure of our past and current approaches. If humans are to thrive at present population levels within portions of the basin, we will need to look more at multiple scales of ecosystem management and at integrating that management to sustain productivity over very long time frames.

The challenge, then, for the people of Washington and Oregon and the whole North Pacific Rim is to recognize that the character and the health of the northern Pacific Basin sub-ecosystems depend upon the material and energy flow processes that link them. The flows of energy and of organic and inorganic materials among the various aquatic and upland ecosystems determines the productivity of each component and of the whole. In short, the whole is greater than the sum of the parts, symbiosis on a grand scale. Understanding the biological processes and the impacts of our management practices upon them will be necessary for our long-term (measured in generations) success in the region. To do that we will need to look beyond the plants, animals, and the habitats of a given smaller scale ecosystem to the processes that link them together, perhaps into the large scale ecosystem of the anadromous salmon. The flow of sediments, woody debris, detritus, and nutrients through a watershed determines the character and productivity of the entire watershed, estuary, the near shore zone and even the domains of the northern Pacific Ocean. The flow of energy and nutrients back upstream via the Pacific salmon and the ability of the watershed to retain them, in large measure, determines the productivity of the entire watershed.

IMPLICATIONS FOR FISHERIES MANAGEMENT

Harvest management of anadromous salmon stocks along the Pacific coast has generally been governed by strictly density dependent policies, in which escapement of spawning fish is maintained at the level which is predicted to generate the greatest number of harvestable fish. This management approach is referred to as maximum sustained yield (MSY). The MSY level is estimated from a relationship between spawning fish and the number of recruits (offspring in the next generation) they produce.

Two models are most commonly employed to describe the relationship between spawning escapement and the population of recruits produced in the next generation for the stock being managed: the Ricker Model [425a] (Figure 17-A) and the Beverton-Holt Model [41a] (Figure 17-B). Both these models assume that the shape of the spawner-recruit relationship is determined primarily by density-dependent interactions. The Ricker model is derived by assuming that the mortality rate of eggs and juveniles is proportional to the initial cohort size and the Beverton-Holt model by assuming that the mortality rate is linearly dependent on the number of fish alive in the cohort at the time. The Ricker model is most often applied to species that compete for spawning space in streams, and the Beverton-Holt model to species that compete for rearing space or food in streams. However, exceptions to this general rule commonly have been found. Chilcote [97a] found that 26 steelhead populations in Oregon, a species for which the Beverton-Holt model would typically be selected as most appropriate because steelhead juveniles compete for rearing space and food in streams, were better fit by a Ricker model. In cases where variable environmental conditions from generation to generation or other factors not related to density-dependent interactions have a major effect on survival; spawner-recruit data may not be adequately described by any model. Because so many physical and biological processes are averaged across the life cycle from spawner to recruit, Hilborn and Walters [204a] have cautioned that it is better to think of spawner-recruit curves as general statistical descriptions rather than something determined from any fundamental biological principle.

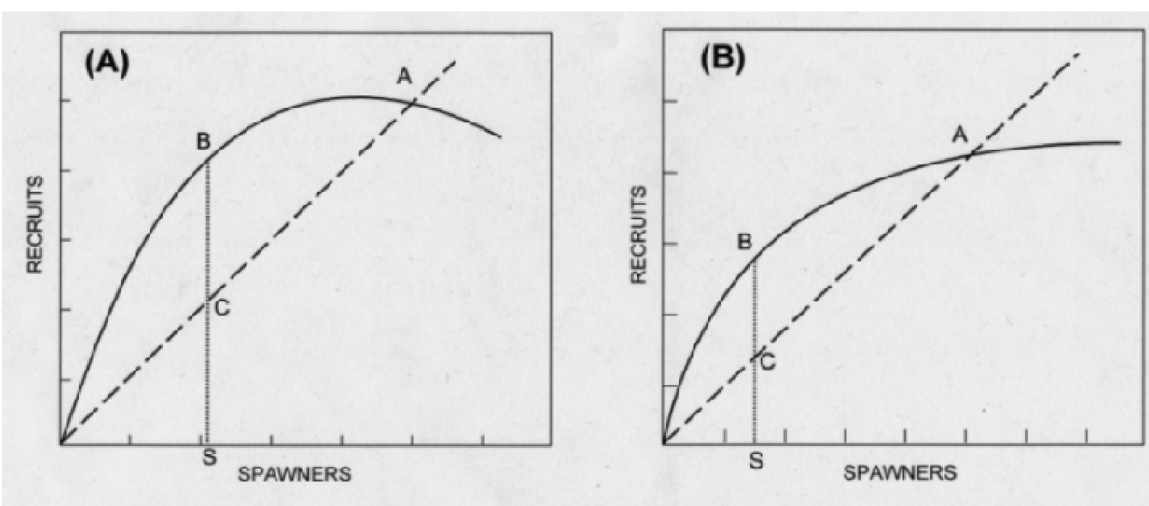

Figure 17. Spawner-recruit curves: (A) Ricker model, (B) Beverton-Holt model.

Regardless of which model is selected, a so-called "replacement line" with a slope = 1 (i.e., one recruit per spawner) is drawn from the origin to intersect and extend beyond the curve. Theoretically, for any level of spawning where the predicted number of recruits is greater than the number needed for spawning, the "surplus" recruits are available for harvest. At the high levels of spawning, the number of recruits produced is less than the spawners required to maintain the population at that level and there are no surplus recruits. The MSY level is defined as the point where the difference between the spawner-recruit curve and the replacement line is greatest, (labeled B and C on the curves in Figures 17-A and 17-B) thus providing the maximum number of harvestable fish. The point where the replacement line intersects the spawner-recruit curve (labeled A on the curves in Figures 17-A and 17-B) represents the equilibrium population level for the stock. Given no harvest of fish and a system with stable environmental conditions over time, the population would migrate towards this point where the number of returning recruits would just replace the number of spawners that produced them. One might think of point A as the natural carrying capacity of the undisturbed system for returning adults.

Although the concept of managing a stock of salmon based on MSY is very appealing, there have been many serious problems encountered in attempting to apply this theory. There are often very high levels of variability in spawner-recruit data. This variability makes selection of the appropriate model to fit the data uncertain making the estimation of key model parameters problematic. As these model parameters are key determinants in the estimation of the MSY level, the setting of escapement goals for stock maintenance based on these models is very risky indeed.

There are well-developed statistical methods that attempt to deal with the variability in spawner-recruit data sets. These procedures can lead to more risk-averse management decisions when using spawner-recruit models (see for example [286a, 514a, 424a]). Even so, the simplifying assumptions underlying the MSY approach cause it to be fraught with other pitfalls. If those making management decisions do not recognize these deficiencies, the true condition of a stock may not be understood until the population suffers a precipitous decline.

Perhaps the greatest source of error in spawner-recruit model estimates is caused by the assumption that density-dependent factors are primarily responsible for determining survival (i.e., number of recruits per spawner). There is ample evidence that environmental factors have a substantial effect on survival of salmon. In the freshwater environment survival may be affected by floods, droughts or declining habitat quality caused by numerous anthropogenic influences [365, 91a]. There is growing evidence that productivity of the northern Pacific Ocean varies cyclically [32, 189], greatly influencing mortality rates in the marine environment [537a]. Thus, controls on mortality rate may be greatly altered by numerous factors that vary in their intensity over time and the effects of which may not be density-dependent.

Considering the above discussion research has revealed that organic matter and nutrients transported to streams by spawning salmon are important for maintaining the productivity of these systems. Nitrogen and carbon contained in rainbow trout residing in a southeast Alaska stream was derived almost entirely from the large numbers of pink salmon which spawned at the site [248]. Juvenile coho salmon, cutthroat trout and steelhead in a tributary of the Snoqualmie River, Washington, obtained as much as 40% of the carbon and nitrogen in their muscle tissue from the carcasses of coho salmon [47]. Johnston et al. [239] found a relationship between the proportion of marine-derived nitrogen in insects and the density of spawning sockeye salmon in tributaries of the Stuart River in interior British Columbia.

Therefore, the productivity of freshwater habitats may be influenced by the abundance of spawning fish using the system.

All age classes and species of fish in the stream utilize the materials transported by spawning salmon [47, 48]. For example, juvenile coho spawned in year N reap the benefits provided by all species of salmon spawning in year N+1 [318, 1]. Conventional spawner-recruit models cannot capture this relationship.

Managing at the MSY level may have the effect of substantially reducing the delivery of marine-derived nutrients to freshwater habitats. Let us assume that a coho population is undisturbed (no harvest) and at equilibrium, and, since coho juveniles compete for rearing space and food in streams, can be modeled by the Beverton-Holt [41a] relationship shown in Figure 18-A. Since this population is undisturbed and at equilibrium, reading off the spawner axis below point A gives the number of spawners whose carcasses would decompose in the stream each cycle to provide nutrients to support the next generation of juveniles. Harvesting this population to the MSY level would reduce the number of spawners, and associated nutrients, to point S on Figure 18-A. This level of spawners represents a reduction of about two-thirds in the number of adult spawners allowed to return to the stream and a corresponding decrease in the level of marine nutrients returned to the stream.

The decreased availability of carcasses has been shown to impact the growth rate of juvenile fishes. Artificially increasing availability of marine-derived materials by adding the carcasses of hatchery-spawned coho salmon to a small stream in southwestern Washington accelerated growth of juvenile coho salmon in this system relative to a nearby stream reach with low availability of carcasses [48]. Coho at the enriched site grew twice as fast as fish at the site without carcasses and achieved a body size nearly 50% greater by early winter. Body size of juvenile salmon has been positively correlated with overwinter survival in freshwater [190a, 414]. Increased smolt size provides a survival advantage in the marine environment [49a, 49b, 215a, 537a, 516a, 214a]. Therefore, if harvest of fish causes a reduction in nutrient delivery to the stream sufficient to impact growth, survival will be negatively impacted. This impact will decrease recruitment to the next generation of spawners, further depleting the nutrient capital of the system and potentially further depressing survival. The effect is a progressive downward shift of the stock-recruitment relationship for each successive cycle. This shift is illustrated in Figure 18-B with the adjusted curve labeled NEW. The possibility that the spawner-recruit relationship could be fundamentally altered due to management decisions is never taken into account in setting harvest levels.

If it were only a matter of stream productivity loss, restoring lost stream productivity might eventually reproduce the same run size. But unanticipated over harvest in any cycle is tantamount to reducing the capacity of the system as well, which down-shifts the stock-recruitment relationship in the manner illustrated in Figure 18-C, so that eventual run size also declines.

Another important factor ignored by spawner-recruit models is the loss of stock productivity related to loss of genetic variability. Loss of genetic variability can reduce survival and mean fitness of a population [141a]. Geiger et al. [165a] reported that there is a link between genetic variability and the level of exploitable production in Alaskan pink salmon populations. They showed that a relatively small proportion of the breeding population is the most productive in any one generation and that the genetic composition of this productive segment changes between generations. This process appears to be true for coho salmon as well [304a], and Geiger et al.[165a] suggest that it may be true for salmon in general. As Ricker and Beverton-Holt models only incorporate total population size, and not population-segment specific contributions to recruitment, they cannot predict decreases in overall stock productivity that result from decreased genetic variability. Harvest policies and practices that inadvertently reduce or eliminate small population segments would decrease genetic variability and could impact stock productivity.

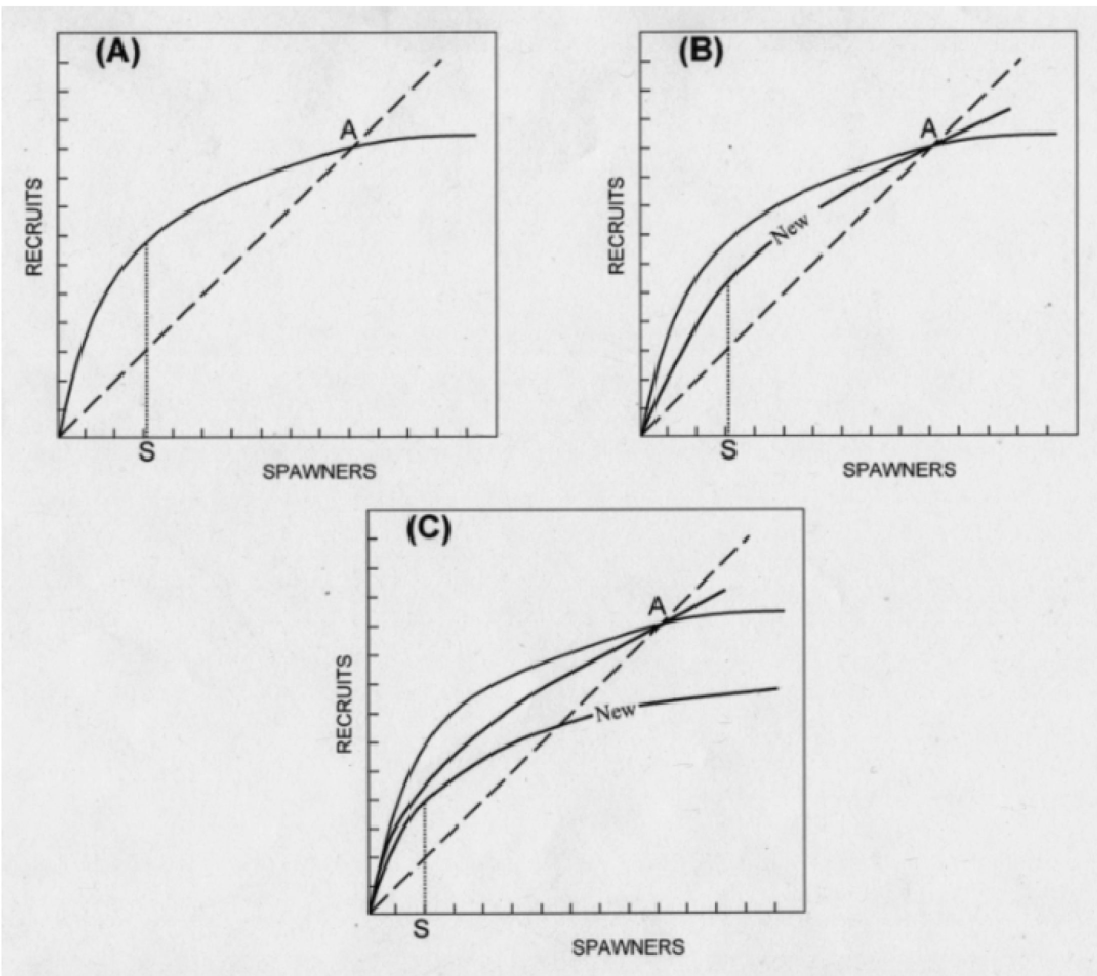

Figure 18. Spawner-recruit curves showing the undisturbed population (A); the same population with a loss in productivity (B); and the same population with an additional loss in capacity (C).

There is increased interest in the Pacific Northwest in developing harvest management strategies that address nutrient delivery to freshwater ecosystems [266, 544]. However, there is relatively little information on which to base escapement targets that will meet this objective. Ideally, estimates of the number of spawners needed to fulfill this function would be determined by experimentally altering escapement levels for each stock and evaluating the impact on system productivity. However, conducting such an experiment on hundreds or thousands of stocks over a sufficient length of time is a daunting prospect and would not provide usable results for many years. Several other approaches to determining appropriate escapement levels are currently being investigated. One option being considered attempts to determine the amount of food required to support a population of rearing fish that fully utilizes the habitat available in a stream. Escapement levels would be established which ensure sufficient nutrients and organic matter are returned to the stream to produce this level of food. Another alternative is to develop a relationship between spawner density and the proportion of marine-derived nutrients in the tissues of juvenile fish. This type of relationship may enable a “saturation level” for marine nutrients to be established and escapement goals set accordingly. However, these approaches do not account for impacts associated with land use that drive down stock productivity (reduce survivals) and reduced habitat capacity, and decreased genetic diversity, nor do they incorporate any consideration of temporal variability in environmental conditions. Nonetheless, these approaches do represent a shift from MSY to more ecologically-based stock management objectives.

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Appendix I. The 9 wildlife species identified as having (or historically had) a *strong, consistent* relationship with salmon in Oregon and Washington. An "x" identifies the life stage(s) of salmon applicable to the species.

	Incubtion	*Freshwater Rearing*	*Saltwater*	*Spawning*	*Carcass*	*Comments*
Common Merganser	x	x	x			
Harlequin Duck	x		x			Strong relationship w/ drift eggs and alevin; indirect relationship w/ carcass-derived insects
Osprey		x	x	x		
Bald Eagle			x	x	x	Strong relationship w/ salmon; also indirect relationship -- feeds on gulls, terns, and waterfowl that eat salmon; occasionally have been seen catching and consuming smolts.
Caspian Tern		x	x			
Black Bear				x	x	
Grizzly Bear				x	x	
Northern River Otter		x		x	x	
Killer Whale			x			

Appendix II. The 58 wildlife species identified as having (or historically had) a *recurrent* relationship with salmon in Oregon and Washington. An "x" identifies the life stage(s) of salmon applicable to the species.

	Incubtion	*Freshwater Rearing*	*Saltwater*	*Spawning*	*Carcass*	*Comments*
Cope's Giant Salamander	x	x			?	Also potential occasional relationship w/ carcasses
Pacific Giant Salamander	x	x				
Pacific Coast Aquatic Garter Snake	x	x				
Red-throated Loon		x	x			
Pacific Loon			x			Also potential relationship with spawning salmon or carcasses
Common Loon		x	x			Also potential relationship with spawning salmon or carcasses
Pied-billed Grebe		x				
Western Grebe		x	x			
Clark's Grebe			x			
American White Pelican		x				
Brandt's Cormorant		x	x			
Double-crested Cormorant		x	x			
Pelagic Cormorant		x	x			
Great Blue Heron		x	x			
Black-crowned Night-heron		x	x			
Turkey Vulture					x	
California Condor					x	A historic relationship based on 1800's literature and archaeological evidence
Common Goldeneye	x	x			x	
Barrow's Goldeneye	x	x			x	
Common Merganser					x	
Red-breasted Merganser	x	x	x			
Golden Eagle				x	x	

Bonaparte's Gull	x		x		x	
Heermann's Gull			x			
Ring-billed Gull		x	x		x	
California Gull			x		x	
Herring Gull		x	x		x	
Thayer's Gull			x			
Western Gull			x		x	
Glaucous-winged Gull	x		x	x	x	
Glaucous Gull			x		x	
Common Tern		x	x			
Arctic Tern		x	x			
Forster's Tern		x	x			
Elegant Tern			x			
Common Murre			x			
Marbled Murrelet		x	x			
Rhinoceros Auklet			x			
Tufted Puffin			x			
Belted Kingfisher		x	x	x		
American Dipper	x	x			x	Direct relationship w/ drift eggs and fry; indirect relationship with carcass-derived insects
Steller's Jay					x	
Black-billed Magpie		x			x	
American Crow		x			x	
Northwestern Crow		x	x		x	
Common Raven		x		x	x	
Virginia Opossum					x	
Water Shrew	x	x			x	May eat drift eggs, fry; indirect relationship with carcass-derived insects
Coyote					x	
Gray Wolf				x	x	
Raccoon		x			x	
Mink		x		x	x	

Bobcat				x	x	
Northern Fur Seal			x			
Northern (Steller) Sea Lion			x	x	x	
California Sea Lion			x	x		
Harbor Seal			x	x	x	
Pacific White-sided Dolphin			x			

Appendix III. The 25 wildlife species identified as having an *indirect* relationship with salmon in Oregon and Washington. An "x" identifies the life stage(s) of salmon applicable to the species.

	Incubtion	*Freshwater Rearing*	*Saltwater*	*Spawning*	*Carcass*	*Comments*
Harlequin Duck					x	Indirect relationship w/ carcass-derived insects; direct relationship w/ eggs
Bald Eagle	x	x	x		x	Indirect relationship -- feeds on gulls, terns, and waterfowl that eat salmon; also strong, direct relationship w/ salmon
Gyrfalcon		x	x		x	Feeds on waterfowl and gulls that eat fish
Peregrine Falcon		x	x		x	Feeds on waterfowl and gulls that eat fish
Killdeer					x	Carcass nutrients support insect supply
Spotted Sandpiper					x	Carcass nutrients support insect supply
Snowy Owl		x				Feeds on waterfowl that eat fish
Willow Flycatcher					x	Carcass nutrients likely to support insect supply
Tree Swallow					x	Carcass nutrients likely to support insect supply
Violet-green Swallow					x	Carcass nutrients likely to support insect supply
Northern Rough-winged Swallow					x	Carcass nutrients likely to support insect supply
Bank Swallow					x	Carcass nutrients likely to support insect supply
Cliff Swallow					x	Carcass nutrients likely to support insect supply
Barn Swallow					x	Carcass nutrients likely to support insect supply
American Dipper					x	Indirect relationship with carcass-derived insects; direct relationship w/ drift eggs and fry
Masked Shrew					x	Likely to eat both carcass meat and insects associated w/ carcasses
Vagrant Shrew					x	Likely to eat both carcass meat and insects associated w/ carcasses
Montane Shrew					x	Likely to eat both carcass meat and insects associated w/ carcasses
Fog Shrew					x	Likely to eat both carcass meat and insects associated w/ carcasses

Pacific Shrew					x	Likely to eat both carcass meat and insects associated w/ carcasses
Water Shrew					x	May eat drift eggs, fry; indirect relationship with carcass-derived insects
Pacific Water Shrew					x	Likely to eat both carcass meat and insects associated w/ carcasses
Trowbridge's Shrew					x	Likely to eat both carcass meat and insects associated w/ carcasses
Harbor Porpoise			x			Feeds on species that feed on smolts
Dall's Porpoise			x			Feeds on species that feed on smolts

Appendix IV. The 65 wildlife species identified as having (or historically had) a *rare* relationship with salmon in Oregon and Washington. An "x" identifies the life stage(s) of salmon applicable to the species.

	Incubation	*Freshwater Rearing*	*Saltwater*	*Spawning*	*Carcass*	*Comments*
Snapping Turtle		x				
Western Pond Turtle		x				
Western Terrestrial Garter Snake		x				
Common Garter Snake		x				
Pacific Loon					x	
Common Loon					x	
Yellow-billed Loon			x			
Horned Grebe	x		x			
Red-necked Grebe			x		x	
Western Grebe					x	
Sooty Shearwater			x			
Brown Pelican			x			
Great Egret		x	x			
Snowy Egret		x				
Green Heron		x	x			
Trumpeter Swan	x	x			x	
Mallard	x				x	
Green-winged Teal	x					
Canvasback					x	
Greater Scaup	x				x	
Surf Scoter			x		x	
White-winged Scoter			x		x	
Common Goldeneye			x		x	
Barrow's Goldeneye			x			

	Incubation	*Freshwater Rearing*	*Saltwater*	*Spawning*	*Carcass*	*Comments*
Hooded Merganser	x	x			x	
Red-tailed Hawk					x	
Greater Yellowlegs	x					
Franklin's Gull		x				
Mew Gull	x					
Black-legged Kittiwake			x		x	
Pigeon Guillemot			x			
Ancient Murrelet			x			
Gray Jay					x	
Winter Wren					x	
American Robin	x					
Varied Thrush	x				x	
Spotted Towhee					x	
Song Sparrow					x	
Masked Shrew					x	Likely to eat both carcass meat and insects associated w/ carcasses
Vagrant Shrew					x	Likely to eat both carcass meat and insects associated w/ carcasses
Montane Shrew					x	Likely to eat both carcass meat and insects associated w/ carcasses
Fog Shrew					x	Likely to eat both carcass meat and insects associated w/ carcasses
Pacific Shrew					x	Likely to eat both carcass meat and insects associated w/ carcasses
Pacific Water Shrew					x	
Trowbridge's Shrew					x	

	Incubation	*Freshwater Rearing*	*Saltwater*	*Spawning*	*Carcass*	*Comments*
Douglas' Squirrel					x	
Northern Flying Squirrel					x	
Deer Mouse					x	
Red Fox					x	
Gray Fox					x	
Ringtail					x	
American Marten					x	
Fisher					x	
Long-tailed Weasel					x	
Wolverine					x	
Striped Skunk					x	
Mountain Lion				x	x	
White-tailed Deer					x	
Black-tailed Deer					x	
Minke Whale			x			
Sperm Whale			x			
Humpback Whale			x			
Northern Right-whale Dolphin			x			
Dall's Porpoise			x			
Harbor Porpoise			x			

Appendix V. The 60 wildlife species identified as having an *unknown* relationship with salmon in Oregon and Washington.

Baird's Shrew	Hoary Bat	Rough-skinned Newt
Big Brown Bat	Keen's Myotis	Short-billed Dowitcher
Black Phoebe	Least Flycatcher	Shrew-mole
Brazilian Free-tailed Bat	Little Brown Myotis	Silver-haired Bat
Brewer's Blackbird	Long-eared Myotis	Southern Torrent Salamander
Bullfrog	Long-legged Myotis	Spotted Bat
California Myotis	Long-toed Salamander	Tailed Frog
Cascade Torrent Salamander	Merriam's Shrew	Townsend's Big-eared Bat
Columbia Torrent Salamander	Northern Leopard Frog	Townsend's Chipmunk
Columbian Mouse	Northern Waterthrush	Townsend's Vole
Cordilleran Flycatcher	Northwestern Salamander	Van Dyke's Salamander
Dunlin	Olympic Torrent Salamander	Warbling Vireo
Dunn's Salamander	Oregon Spotted Frog	Water Vole
Dusky Flycatcher	Pacific-slope Flycatcher	Western Pipistrelle
Ermine	Painted Turtle	Western Sandpiper
European Starling	Pallid Bat	Western Small-footed Myotis
Foothill Yellow-legged Frog	Purple Martin	Western Spotted Skunk
Fringed Myotis	Pygmy Shrew	Western Toad
Gray Catbird	Red-eared Slider Turtle	Woodhouse's Toad
Hammond's Flycatcher	Red-legged Frog	Yuma Myotis

Appendix VI. The 407 wildlife species identified as having (or historically had) *no* relationship with salmon in Oregon and Washington.

Acorn Woodpecker
Aleutian Canada Goose
Allen's Chipmunk
Allen's Hummingbird
American Avocet
American Badger
American Beaver
American Bittern
American Black Duck
American Coot
American Golden-Plover
American Goldfinch
American Kestrel
American Pika
American Pipit
American Redstart
American Tree Sparrow
American Wigeon
Anna's Hummingbird
Ash-throated Flycatcher
Baird's Sandpiper
Band-tailed Pigeon
Barn Owl
Barred Owl
Belding's Ground Squirrel
Bewick's Wren
Bison
Black Oystercatcher
Black Rat
Black Rosy-finch
Black Salamander
Black Scoter
Black Swift
Black Tern
Black Turnstone
Black-backed Woodpecker
Black-bellied Plover
Black-capped Chickadee
Black-chinned Hummingbird
Black-footed Albatross
Black-headed Grosbeak
Black-necked Stilt
Black-tailed Jackrabbit
Black-throated Gray Warbler
Black-throated Sparrow
Blue Grouse
Blue Whale
Blue-gray Gnatcatcher
Blue-winged Teal
Bobolink
Bohemian Waxwing
Boreal Chickadee
Boreal Owl
Botta's (Pistol River) Pocket Gopher
Brant
Brewer's Sparrow
Broad-footed Mole
Broad-tailed Hummingbird
Brown Creeper
Brown-headed Cowbird
Brush Rabbit
Buff-breasted Sandpiper
Bufflehead
Buller's Shearwater
Bullock's Oriole
Burrowing Owl
Bushtit
Bushy-tailed Woodrat
Cackling Canada Goose
California Bighorn Sheep
California Ground Squirrel
California Kangaroo Rat
California Mountain Kingsnake
California Quail
California Slender Salamander
California Towhee
California Vole
Calliope Hummingbird
Camas Pocket Gopher
Canyon Mouse
Canyon Wren
Cascade Golden-mantled Ground Squirrel
Cascades Frog
Cassin's Auklet
Cassin's Finch
Cassin's Vireo
Cattle Egret
Cedar Waxwing
Chestnut-backed Chickadee
Chipping Sparrow
Chisel-toothed Kangaroo Rat
Chukar
Cinnamon Teal
Clark's Nutcracker
Clay-colored Sparrow
Clouded Salamander
Coast Mole
Columbia Spotted Frog
Columbian Ground Squirrel
Columbian White-tailed Deer
Common Kingsnake
Common Nighthawk
Common Poorwill
Common Porcupine
Common Redpoll
Common Snipe
Common Yellowthroat
Cooper's Hawk
Creeping Vole
Dark Kangaroo Mouse
Dark-eyed Junco
Del Norte Salamander
Desert Horned Lizard
Desert Woodrat
Downy Woodpecker
Dusky Canada Goose
Dusky-footed Woodrat
Eared Grebe
Eastern Cottontail
Eastern Fox Squirrel
Eastern Gray Squirrel
Eastern Kingbird
Ensatina
Eurasian Wigeon
European Rabbit
Evening Grosbeak
Feral Horse
Feral Pig
Ferruginous Hawk
Flammulated Owl
Flesh-footed Shearwater
Fork-tailed Storm-petrel
Fox Sparrow
Gadwall
Giant Canada Goose
Golden-crowned Kinglet
Golden-crowned Sparrow
Golden-mantled Ground Squirrel
Gopher Snake
Grasshopper Sparrow
Gray Flycatcher
Gray Partridge
Gray Whale
Gray-crowned Rosy-Finch
Gray-tailed Vole
Great Basin Pocket Mouse
Great Basin Spadefoot
Great Gray Owl
Great Horned Owl
Greater White-fronted Goose
Green Frog
Green-tailed Towhee
Hairy Woodpecker

Harris's Sparrow
Heather Vole
Hermit Thrush
Hermit Warbler
Hoary Marmot
Horned Lark
House Finch
House Mouse
House Sparrow
House Wren
Hutton's Vireo
Juniper Titmouse
Kit Fox
Lapland Longspur
Larch Mountain Salamander
Lark Sparrow
Laysan Albatross
Lazuli Bunting
Leach's Storm-petrel
Least Bittern
Least Chipmunk
Least Sandpiper
Leatherback Turtle
Lesser Canada Goose
Lesser Goldfinch
Lesser Scaup
Lesser Yellowlegs
Lewis's Woodpecker
Lincoln's Sparrow
Little Pocket Mouse
Loggerhead Shrike
Long-billed Curlew
Long-billed Dowitcher
Long-eared Owl
Long-nosed Leopard Lizard
Long-tailed Jaeger
Long-tailed Vole
Lynx
Macgillivray's Warbler
Marbled Godwit
Marsh Wren
Meadow Vole
Merlin
Merriam's Ground Squirrel
Mojave Black-collared Lizard
Montane Vole
Moose
Mountain Beaver
Mountain Bluebird
Mountain Caribou
Mountain Chickadee
Mountain Goat
Mountain Quail
Mourning Dove
Mule Deer
Muskrat
Mute Swan
Nashville Warbler
Night Snake
North Pacific Bottle-nosed Whale
Northern Alligator Lizard
Northern Bobwhite
Northern Bog Lemming
Northern Elephant Seal
Northern Flicker
Northern Fulmar
Northern Goshawk
Northern Grasshopper Mouse
Northern Harrier
Northern Mockingbird
Northern Pintail
Northern Pocket Gopher
Northern Pygmy-owl
Northern Saw-whet Owl
Northern Shoveler
Northern Shrike
Northwestern Garter Snake
Norway Rat
Nutria
Nuttall's (Mountain) Cottontail
Oak Titmouse
Oldsquaw
Olive-sided Flycatcher
Olympic Marmot
Orange-crowned Warbler
Ord's Kangaroo Rat
Oregon Slender Salamander
Pacific Golden-Plover
Pacific Jumping Mouse
Pacific Treefrog
Palm Warbler
Parasitic Jaeger
Pectoral Sandpiper
Pileated Woodpecker
Pine Grosbeak
Pine Siskin
Pink-footed Shearwater
Pinon Mouse
Pinyon Jay
Piute Ground Squirrel
Plateau Striped Whiptail
Plumbeous Vireo
Pomarine Jaeger
Prairie Falcon
Preble's Shrew
Pronghorn Antelope
Purple Finch
Pygmy Nuthatch
Pygmy Rabbit
Racer
ed Crossbill
Red Knot
Red Phalarope
Red Squirrel
Red Tree Vole
Red-breasted Nuthatch
Red-breasted Sapsucker
Red-eyed Vireo
Redhead
Red-naped Sapsucker
Red-necked Phalarope
Red-shouldered Hawk
Red-tailed Chipmunk
Red-winged Blackbird
Ringneck Snake
Ring-necked Duck
Ring-necked Pheasant
Risso's Dolphin
Rock Dove
Rock Sandpiper
Rock Wren
Rocky Mountain Bighorn Sheep
Rocky Mountain Elk
Roosevelt Elk
Ross's Goose
Rough-legged Hawk
Rubber Boa
Ruby-crowned Kinglet
Ruddy Duck
Ruddy Turnstone
Ruff
Ruffed Grouse
Rufous Hummingbird
Sabine's Gull
Sage Grouse
Sage Sparrow
Sage Thrasher
Sagebrush Lizard
Sagebrush Vole
Sanderling
Sandhill Crane
Savannah Sparrow
Say's Phoebe
Scaled Quail
Sea Otter
Semipalmated Plover
Semipalmated Sandpiper
Sharp-shinned Hawk
Sharptail Snake
Sharp-tailed Grouse
Sharp-tailed Sandpiper
Short-eared Owl
Short-finned Pilot Whale
Short-horned Lizard
Short-tailed Albatross
Short-tailed Shearwater
Side-blotched Lizard

Siskiyou Chipmunk
Siskiyou Mtns. Salamander
Sky Lark
Snow Bunting
Snow Goose
Snowshoe Hare
Snowy Plover
Solitary Sandpiper
Sora
South Polar Skua
Southern Alligator Lizard
Southern Red-backed Vole
Spotted Owl
Spruce Grouse
Stilt Sandpiper
Striped Whipsnake
Surfbird
Swainson's Hawk
Swainson's Thrush
Swamp Sparrow
Taverner's Canada Goose
Three-toed Woodpecker
Tiger Salamander
Townsend's Ground Squirrel
Townsend's Mole
Townsend's Pocket Gopher
Townsend's Solitaire
Townsend's Warbler
Tricolored Blackbird
Tundra Swan
Upland Sandpiper
Vancouver Canada Goose
Vaux's Swift
Veery
Vesper Sparrow
Virginia Rail
Wandering Tattler
Washington Ground Squirrel
Western Bluebird
Western Canada Goose
Western Fence Lizard
Western Gray Squirrel
Western Ground Snake
Western Harvest Mouse
Western Jumping Mouse
Western Kingbird
Western Meadowlark
Western Pocket Gopher
Western Rattlesnake
Western Red-backed Salamander
Western Red-backed Vole
Western Screech-owl
Western Scrub-Jay
Western Skink
Western Tanager
Western Whiptail
Western Wood-pewee
Whimbrel
White-breasted Nuthatch
White-crowned Sparrow
White-faced Ibis
White-footed Vole
White-headed Woodpecker
White-tailed Antelope Squirrel
White-tailed Jackrabbit
White-tailed Kite
White-tailed Ptarmigan
White-throated Sparrow
White-throated Swift
White-winged Crossbill
Wild Burro
Wild Turkey
Willet
Williamson's Sapsucker
Wilson's Phalarope
Wilson's Warbler
Wood Duck
Wrentit
Wyoming Ground Squirrel
Yellow Rail
Yellow Warbler
Yellow-bellied Marmot
Yellow-billed Cuckoo
Yellow-breasted Chat
Yellow-headed Blackbird
Yellow-pine Chipmunk
Yellow-rumped Warbler

Appendix VII. List of published and unpublished observations of wildlife predation and scavenging on salmon.

Salmon life stage	Species	Relationship to salmon	References	Location of study/report
INCUBATION – EGGS AND ALEVIN	Cope's Giant Salamander	Recurrent	Johnson et al. 2000	
	Pacific Giant Salamander	Recurrent	Graf 1949	California
	Pacific Coast Aquatic Garter Snake	Recurrent	Brown et al. 1995	Oregon
	Common Merganser	Strong	Munro and Clemens 1932, 1937, 1939	British Columbia
	Hooded Merganser	Rare	Reimchen 1994	British Columbia
	Red-breasted Merganser	Recurrent	Munro and Clemens 1939	Canada
	Barrow's Goldeneye	Recurrent	Willson and Halupka 1995	Alaska
			Munro 1938, 1939	British Columbia
	Common Goldeneye	Recurrent	Willson and Halupka 1995	Alaska
			Munro 1938, 1939	British Columbia
	American Dipper	Recurrent	Ehinger 1930	Washington
			Munro 1923, Obermayer et al. 1999, Piorkowski 1995, Willson and Halupka 1995	Alaska
			Reimchen 1994, Burcham 1904	British Columbia
	Glaucous-winged Gull	Recurrent	Baird 1990	Washington
			Reimchen 1994	British Columbia
			Mossman 1958, Moyle 1966	Alaska
	Bonaparte's Gull	Recurrent	Moyle 1966	Alaska
	Harlequin Duck	Strong	Dzinbal and Jarvis 1982, Obermayer et al. 1999	Alaska
	Horned Grebe	Rare	Palmer 1962	Washington
			Munro 1941	British Columbia
	Trumpeter Swan	Rare	Farley 1980	Alaska
	Mallard	Rare	Willson and Halupka 1995	Alaska
	Green-winged Teal	Rare	Ned Pittman, pers. comm.	Washington
	Greater Scaup	Rare	Munro 1941	British Columbia
	Greater Yellowlegs	Rare	Elphick and Tibbitts 1998	Alaska
	Mew Gull	Rare	Moyle 1966	Alaska
	American Robin	Rare	Willson and Halupka 1995	Alaska

	Varied Thrush	Rare	Ned Pittman pers. comm.	Washington
	Water Shrew	Recurrent	Banfield 1974	Canada
FRESHWATER REARING – FRY AND PARR	Cope's Giant Salamander	Recurrent	Antonelli et al. 1972	Washington
	Pacific Giant Salamander	Recurrent	Antonelli et al. 1972	Washington
			Parker 1993, Parker 1994	California
	Snapping Turtle	Rare	Johnson and Hasler 1954, Lagler 1943	Michigan
	Western Pond Turtle	Rare	Johnson et al. 2000	
	Pacific Coast Aquatic Garter Snake	Recurrent	Brown et al. 1995, Fitch 1941, 1984, Drummond 1983 Hansen 1980	Oregon, California
	Western Terrestrial Garter Snake	Rare	Anderson 1977, Tanner 1949	Montana, Utah
	Common Garter Snake	Rare	Lagler and Salyer 1945	Michigan
	Red-throated Loon	Recurrent	Eriksson et al. 1990	Sweden
			Palmer 1962	Labrador
	Common Loon	Recurrent	Palmer 1962, Johnson and Hasler 1954, Alexander 1977	Michigan
			Fraser 1972, 1974, Matkowski 1989, Matkowski 1984, Barr 1973, Smith 1968, Munro 1945	Canada, British Columbia
			Willson and Halupka 1995	Alaska
	Pied-billed Grebe	Recurrent	Zarnowitz and Raedeke 1984	Washington
	Western Grebe	Recurrent	Modde and Wasowicz 1996	Utah
	American White Pelican	Recurrent	Myers and Peterka 1976, Lingle 1977	North Dakota
			Palmer 1962	Wyoming
	Brandt's Cormorant	Recurrent	Johnson et al. 2000	
	Double-crested	Recurrent	Modde and Wasowicz 1996	Utah
			Mayers and Peterka 1976	North Dakota
	Pelagic Cormorant	Recurrent	Johnson et al. 2000	
	Great Blue Heron	Recurrent	Alexander 1977, 1979, Bent 1926, Johnson and Hasler 1954	Michigan
			Fraser 1972, Matkowski 1989, Smith 1968	Canada
			Dolloff 1993, Willson and Halupka 1995	Alaska
			Zarnowitz and Raedeke 1984	Washington
			Henney and Bethers 1971	Oregon

FRESHWATER REARING – FRY AND PARR	Great Egret	Rare	Johnson et al. 2000	
	Snowy Egret	Recurrent	Johnson et al. 2000	
	Green Heron	Rare	Jurek 1974	California
	Black-crowned Night	Recurrent	Spanier 1980	Israel
			Myers and Peterka 1976	North Dakota
	Trumpeter Swan	Rare	Farley 1980	Alaska
			Hampton 1981	Montana
	Common Goldeneye	Recurrent	Beach 1937	Michigan
			White 1939	Nova Scotia
	Barrow's Goldeneye	Recurrent	Munro and Clemens 1938, 1939	British Columbia
	Hooded Merganser	Rare	Zarnowitz and Raedeke 1984	Washington
	Common Merganser	Strong	Alexander 1977, 1979, Beach 1937, Johnson and Halser 1954, Salyer and Lagler 1940, Shetter 1970	Michigan
			Miegs and Rieck 1967, Senn 1958	Washington
			Fraser 1972, Huntsman 1941, Munro and Clemens 1932, 1937, 1939, Smith 1968	Canada
			Willson and Halupka 1995	Alaska
			White 1936, 1957	Nova Scotia
	Red-breasted merganser	Recurrent	Munro and Clemens 1939	Canada
			Marquiss and Duncan 1993	Scotland
	Osprey	Strong	Swenson 1978	Wyoming
			Steeger et al. 1992	British Columbia
			MacCarter 1972	Montana
			Johnson and Hasler 1954	Michigan
			Van Daele and Van Daele 1982	Idaho
			French and Koplin 1977	California
			Hughes 1983	Alaska
			Lind 1976	Oregon
	Franklin's Gull	Rare	Myers and Peterka 1976	North Dakota
	Ring-billed Gull	Recurrent	Nui Tateyama, pers. comm.	Washington
	Caspian Tern	Strong	Johnson et al. 2000	

FRESHWATER REARING – FRY AND PARR	Herring Gull	Recurrent	Mendall 1939	Maine
	Forster's Tern	Recurrent	Ayles et al. 1976	Canada
	Common Tern	Recurrent	Ayles et al. 1976	Canada
	Arctic Tern	Recurrent	Mossman 1959, Willson and Halupka 1995	Alaska
	Marbled Murrelet	Recurrent	Brooks 1928	British Columbia
			Carter and Sealy 1984	Alaska
	Belted Kingfisher	Recurrent	Alexander 1977, 1979	Michigan
			Willson and Halupka 1995	Alaska
			Gould 1934, Eipper 1956	New York
			White 1936	Nova Scotia
			Elson 1962, Huntsman 1941	Canada
	Black-billed Magpie	Recurrent	Willson and Halupka 1995	Alaska
	American Crow	Recurrent	Willson and Halupka 1995	Alaska
	Northwestern Crow	Recurrent	Willson and Halupka 1995	Alaska
	Common Raven	Recurrent	Johnson et al. 2000	
	American Dipper	Recurrent	Dolloff 1993	Alaska
			Loegering 1997	Oregon
			Thut 1970	Washington
			Kingery 1996, Cottam and Uhler 1937	British Columbia
	Water Shrew	Recurrent	Lampman 1947	Oregon
			Banfield 1974	Canada
			Conaway 1952	Montana
	Raccoon	Recurrent	Alexander 1977	Michigan
	Mink	Recurrent	Whitman 1981	Idaho
			Dunstone 1993	New York
			Banfield 1974, Burgess and Bider 1980, Fraser 1972	Canada
			Ben-David et al. 1997	Alaska
			Grinnell et al. 1937	California
			Alexander 1977, 1979	Michigan
			Akande 1972	Scotland
	Northern River Otter	Strong	Zarnowitz and Raedeke 1984	Washington

FRESHWATER – FRY AND PARR		Strong	Banfield 1974, Stenson et al. 1984	British Columbia
			Dolloff 1993	Alaska
			Alexander 1979	Michigan
SALTWATER – SMOLT, IMMATURE ADULTS AND ADULTS	Pacific Loon	Recurrent	Mace 1983	British Columbia
	Red-throated Loon	Recurrent	Johnson et al. 2000	
	Common loon	Recurrent	Palmer 1962	Alaska
			Mace 1983	British Columbia
	Yellow-billed Loon	Rare	North 1994	Russia
	Horned Grebe	Rare	Mace 1983, Vermeer 1992	British Columbia
	Red-necked Grebe	Rare	Mace 1983	British Columbia
	Western Grebe	Recurrent	Vermeer et al. 1992, Mace 1983	British Columbia
	Clark's Grebe	Recurrent	Johnson et al. 2000	
	Sooty Shearwater	Rare	Emmett 1997, Bayer 1989	Oregon
	Brown Pelican	Rare	Bayer 1986a, Emmett 1997, McNeil et al. 1991	Oregon
	Brandt’s Cormorant	Recurrent	Aniley and Sanger 1979	California
			Bayer 1986a, Scott 1973	Oregon
	Double-crested Cormorant	Recurrent	Bayer 1986a, Bayer 1989, Erickson 1988, Hoffman and Hall 1988, Roby et al. 1998	Oregon
			Ainley and Anderson 1981, Mace 1993, Robertson 1974	British Columbia
	Pelagic Cormorant	Recurrent	Bayer 1986a, Scott 1973	Oregon
			Jewett et al. 1953	Washington
			Mace 1983	British Columbia
	Great Blue Heron	Recurrent	Forbes and Simpson 1982, Mace 1983, Myers 1980	British Columbia
	Green Heron	Rare	Johnson et al. 2000	
	Black-crowned Night Heron	Recurrent	Johnson et al. 2000	
	Great Egret	Recurrent	Johnson et al. 2000, Schlorff 1978	California
	Harlequin Duck	Strong	Cottam 1939, Mace 1983	British Columbia
	Surf Scoter	Rare	Mace 1983	British Columbia
	White-winged Scoter	Rare	Mace 1983	British Columbia
	Common Goldeneye	Rare	Mace 1983	British Columbia
	Barrow's Goldeneye	Rare	Mace 1983	British Columbia

SALTWATER – SMOLT, IMMATURE ADULTS AND ADULTS	Common Merganser	Strong	Elson 1962	Canada
			Mace 1983, Macdonald et al. 1988, Wood and Hand 1985, Wood 1985, 1986, 1987	British Columbia
	Red-breasted Merganser	Recurrent	Mace 1983	British Columbia
	Osprey	Strong	Bayer 1986a, Emmett 1997, Roby et al. 1998	Oregon
	Bald Eagle	Recurrent	Knight et al. 1990, Watson et al. 1991	Washington
	Bonaparte's Gull	Recurrent	Macdonald et al. 1988, Mace 1983	British Columbia
	Heermann's Gull	Recurrent	Bayer 1986a, 1989	Oregon
	Ring-billed Gull	Recurrent	Bayer 1989, Roby et al. 1998	Oregon
			Ruggerone 1986	Washington
	California Gull	Recurrent	Roby et al. 1998	Oregon
			Mace 1983	British Columbia
	Herring Gull	Recurrent	Bent 1921	Washington
			Mace 1983, Macdonald et al. 1988	British Columbia
	Thayer's Gull	Recurrent	Mace 1983	British Columbia
	Western Gull	Recurrent	Bayer 1986a, 1986b, Roby et al. 1998	Oregon
	Glaucous-winged Gull	Recurrent	Baird 1990	Washington
			Roby et al. 1998, Bayer 1986a	Oregon
			Mace 1983, Vermeer 1982	British Columbia
	Glaucous Gull	Recurrent	Sanger 1983	Alaska
	Black-legged Kittiwake	Rare	Rowlett 1980, Sanger 1983	Alaska
			Simenstad et al. 1979	Oregon
	Caspian Tern	Strong	Smith and Mudd 1978	Washington
			Roby et al. 1998	Oregon
	Elegant Tern	Recurrent	Johnson et al. 2000	
	Common Tern	Recurrent	Johnson et al. 2000, Simenstad et al. 1979	Oregon
	Forster's Tern	Recurrent	Johnson et al. 2000	
	Arctic Tern	Recurrent	Simenstad et al. 1979	Oregon
			Willson and Halupka 1995	Alaska
	Common Murre	Recurrent	Sydeman et al. 1996	California
			Bayer 1986a, Bayer 1986b, Matthews 1983	Oregon

SALTWATER – SMOLT, IMMATURE ADULTS AND ADULTS			The OR Inst. Of Marine Biol. 1982	Oregon
			Ainley et al. 1990	Alaska
	Pigeon Guillemot	Rare	Bayer 1986a	Oregon
	Marbled Murrelet	Recurrent	DeGange 1996	Alaska
			Mace 1983	British Columbia
	Ancient Murrelet	Rare	Mace 1983	British Columbia
	Rhinoceros Auklet	Recurrent	Wilson and Manuwal 1986	Washington
			Burger et al. 1993, Vermeer and DeVito 1986, Vermeer and Westrheim 1984, Vermeer 1979	British Columbia
			Gaston and Dechesne 1996, Sydeman et al. 1997	California
			Sanger 1983	Alaska
	Tufted Puffin	Recurrent	Baird 1990, 1991, Wehle 1983	Alaska
	Belted Kingfisher	Recurrent	Bayer 1989	Oregon
			Mace 1983	British Columbia
	Northwestern Crow	Recurrent	Mace 1983	British Columbia
	Northern Fur Seal	Recurrent	Antonelis an Perez 1984, Baker et al. 1970, Kajimura 1980	Washington,
			Clemens and Wilby 1933, Spalding 1964	British Columbia
			Scheffer 1950, Wilke and Kenyon 1957	Bering Sea
			Banfield 1974	Canada
			Fiscus and Baines 1966, Imler and Sarber 1947, Pitcher 1981	Alaska
			Dalquest 1948	Washington
			Riemer and Brown 1997, Roffe and Mate 1983	Oregon
			Banfield 1974, Spalding 1964	British Columbia
	California Sea Lion	Recurrent	Gearin et al. 1988, Jeffries 1984	Washington
			Jameson and Kenyon 1977, Riemer and Brown 1997, Roffe and Mate 1983	Oregon
			Baltz and Morejohn 1978, Harvey and Weise 1997, Jones 1981, NMFS 1997	California
	Harbor Seal	Recurrent	Dalquest 1948, Everitt et al. 1981, Sheffer and Sperry 1931, Scheffer and Slipp 1944	Washington

SALTWATER – SMOLT, IMMATURE ADULTS AND ADULTS			Beach et al. 1985, Brown and Mate 1983, Brown et al. 1995, Browne et al. 1997, Graybill 1981, Jeffries 1985, Riemer and Brown 1997, Roffe and Mate 1984	Oregon
			Olesiuk 1993, Olesiuk et al. 1990, Spalding 1964	British Columbia
			Imler and Sarber 1947, Pitcher and Calkins 1981, Pitcher 1977, 1981	Alaska
			Briggs and Davis 1972, Jones 1981, Herder 1983, Hanson 1993	California
	Minke Whale	Rare	Banfield 1974	Canada
			Stewart and Leatherwood 1985	Atlantic Ocean
	Humpback Whale	Rare	Johnson and Wolman 1984	Northern Hemisphere
	Pacific White-sided Dolphin	Recurrent	Kajimura et al. 1980, Stroud et al. 1980	Washington
	Northern Right-Whale Dolphin	Rare	Johnson et al. 2000	
	Killer Whale	Strong	Hall 1986	Alaska
			Scheffer and Slipp 1948	Washington
			Nichol and Shackleton 1996, Banfield 1974	British Columbia
			Balcomb et al. 1982, Heimlich-Boran 1986, 1987, Felleman et al. 1991	Pacific Northwest
	Harbor Porpoise	Rare	Gearin et al. 1994	Washington
			Fontaine et al. 1994	Canada
	Dall's Porpoise	Rare	Norris and Prescott 1961	Oregon
			Mizue et al. 1996	Washington
	Sperm Whale	Rare	Leatherwood and Reeves 1983, Pike 1950	British Columbia
	Osprey	Strong	Johnson et al. 2000	
	Bald Eagle	Strong	Hunt et al. 1992, Servheen 1975, Spencer et al. 1989, Stalmaster 1976	Washington
			Simons 1983	Oregon

SPAWNING			Munro 1938a	British Columbia
			Ofelt 1975	Alaska
	Golden Eagle	Recurrent	McClelland 1973	Montana
	Glaucous-winged Gull	Recurrent	Mossman 1958	Alaska
	Belted Kingfisher	Recurrent	Reimchen 1994	British Columbia
	Common Raven	Recurrent	Reimchen 1994	British Columbia
	Gray Wolf	Recurrent	Young 1944	Alaska
	Black Bear	Strong	Kellyhouse 1975	California
			Reimchen 1994	British Columbia
			Mattson 1989	Idaho
			Chi 1999, Moyle 1966, Piorkowski 1995, Wilson et al. 1998, Frame 1974	Alaska
			Banfield 1974	Canada
	Grizzly Bear	Strong	Banfield 1974	Canada
	Mink	Recurrent	Eagle and Whitman 1987	Canada
			Melquist et al. 1981	Idaho
			Hatler 1976	British Columbia
	Northern River Otter	Strong	Melquist et al. 1981	Idaho
			Toweill 1974	Oregon
	Mountain Lion	Rare	Ned Pittman pers. comm.	Washington
	Bobcat	Recurrent	Yoakum 1964	Washington
	Habor Seal	Recurrent	Reimchen 1994	British Columbia
			Everitt et al. 1981	Washington
			Riemer and Brown 1997	Oregon
	California Sea Lion	Recurrent	Jeffries 1984	Oregon
			Riemer and Brown 1997, Roffe and Mate 1983	Oregon
	Northern (Steller) Sea	Recurrent	Roffe and Mate 1983, Riemer and Brown 1997	Oregon
			Reimchen 1994	British Columbia
CARCASSES	Western Pond Turtle	Rare	Holland 1985	California
	Common Loon	Rare	Reimchen 1994	British Columbia
	Western Grebe	Rare	Reimcher 1994	British Columbia

CARCASSES	Pacific Loon	Rare	Reimchen 1994	British Columbia
	Red-necked Grebe	Rare	Reimchen 1994	British Columbia
	Turkey Vulture	Recurrent	Jewett et al. 1953	Washington
	California Condor	Recurrent	Gabrielson and Jewett 1940, Simons 1983	Oregon
			Suckley and Cooper 1860	Washington
	Trumpeter Swan	Rare	Butler 1973	British Columbia
	Mallard	Rare	Jewett et al. 1953	Washington
			Reimchen 1994	British Columbia
	Canvasback	Rare	Jewett et al. 1953	Washington
	Greater Scaup	Rare	Munro 1941, Reimchen 1994	British Columbia
	Surf Scoter	Rare	Reimchen 1994	British Columbia
	White-winged Scoter	Rare	Reimchen 1994	British Columbia
	Common Goldeneye	Recurrent	Dawson 1909, Jewett et al. 1953, Servheen 1975	Washington
			Taverner 1934	Canada
	Barrow's Goldeneye	Recurrent	Jewett et al. 1953	Washington
	Hooded Merganser	Rare	Reimchen 1994	British Columbia
	Common Merganser	Recurrent	Stalmaster and Gessaman 1984	Washington
			Munro and Clemens 1932, 1937, 1939	British Columbia
	Bald Eagle	Strong	Cederholm et al. 1989Jewett et al. 1953, Knight and Knight 1983, Skagen et al. 1991, Stalmaster and Gessaman 1984, Owen et al. 1990	Washington
			Simons 1983	Oregon
			Munro 1938a	British Columbia
			Frame 1974	Alaska
			Shea 1970	Montana
	Red-tailed Hawk	Rare	Willson and Halupka 1995	Alaska
			Cederholm et al. 1989, Ned Pittman pers. comm., Stalmaster and Gessaman 1984, Stalmaster 1980, Nui Tateyama, pers. comm.	Washington
	Golden Eagle	Recurrent	Stalmaster and Gessaman 1984	Washington
	Ring-billed Gull	Recurrent	Johnson et al. 2000	
	California Gull	Recurrent	Johnson et al. 2000, Reimchen 1994	British Columbia

	Bonaparte's Gull	Recurrent	Moyle 1966, Willson and Halupka 1995, Frame 1974	Alaska
	Western Gull	Recurrent	Johnson et al. 2000	
CARCASSES	Herring Gull	Recurrent	Reimchen 1994	British Columbia
	Glaucous-winged Gull	Recurrent	Reimchen 1994	British Columbia
			Simons 1983	Oregon
			Moyle 1966, Bent 1921, Frame 1974	Alaska
			Servheen 1975, Skagen et al. 1991, Stalmaster and Gessaman 1984	Washington
	Glaucous Gull	Recurrent	Johnson et al. 2000	
	Black-legged Kittiwake	Rare	Reimchen 1994	British Columbia
	Gray Jay	Rare	Cederholm et al. 1989	Washington
	Steller's Jay	Recurrent	Cederholm et al. 1989	Washington
			Willson and Halupka 1995, Frame 1974	Alaska
	Black-billed Magpie	Recurrent	Willson and Halupka 1995	Alaska
			McClelland 1973	Montana
	American Crow	Recurrent	Cederholm et al. 1989, Skagen et al. 1991, Stalmaster and Gessaman 1984	Washington
	Northwestern Crow	Recurrent	Frame 1974	Alaska
			Campbell et al. 1990, Reimchen 1994	British Columbia
	Common Raven	Recurrent	Murie 1959, Willson and Halupka 1995, Frame 1974	Alaska
			Knight and Anderson 1990, Stalmaster and Gessaman 1984, Cederholm et al. 1989, Suckley and Cooper 1860	Washington
	Winter Wren	Rare	Cederholm et al. 1989	Washington
			Reimchen 1994	British Columbia
	American Dipper	Recurrent	Willson and Halupka 1995	Alaska
			Cederholm et al. 1989	Washington
	Varied Thrush	Rare	Reimchen 1994	British Columbia
	Spotted Towhee	Rare	Ned Pittman pers. comm.	Washington
	Song Sparrow	Rare	Ned Pittman pers. comm.	Washington
	Virginia Opossum	Recurrent	Johnson et al. 2000	
	Deer Mouse	Rare	Cederholm et al. 1989	Washington

Douglas' Squirrel	Rare	Cederholm et al. 1989	Washington
Northern Flying Squirrel	Rare	Cederholm et al. 1989	Washington
Water Shrew	Recurrent	Cederholm et al. 1989	Washington
		Conaway 1952	Montana
Vagrant Shrew	Rare	Cederholm et al. 1989	Washington
Masked Shrew	Rare	Cederholm et al. 1989	Washington
Trowbridge's Shrew	Rare	Johnson et al. 2000	
Pacific Water Shrew	Rare	Johnson et al. 2000	
Pacific Shrew	Rare	Johnson et al. 2000	
Montane Shrew	Rare	Johnson et al. 2000	
Fog Shrew	Rare	Johnson et al. 2000	
Coyote	Recurrent	Young 1944	Oregon
		Cederholm et al. 1989, Stalmaster and Gessaman 1984	Washington
Gray Wolf	Recurrent	Young 1944	Oregon, British
Red Fox	Rare	Young 1944	Oregon
		Willson and Halupka 1995	Alaska
		Hewson 1995	Scotland
Gray Fox	Rare	Young 1944	Oregon
Black Bear	Strong	Young 1944	British Columbia
		Piorkowski 1995, Chi 1999, Frame 1974	Alaska
		Cederholm et al. 1989, Hilderbrand et al. 1996	Washington
Grizzly Bear	Strong	Mattson et al. 1991	Idaho
		Hamilton and Archibald 1985, Hamilton and Bunnel 1987, Young 1944	British Columbia
		Banfield 1974	Canada
		Verts and Carraway 1998	Oregon
Ringtail	Rare	Johnson et al. 2000	
Raccoon	Recurrent	Cederholm et al. 1989	Washington
American Marten	Rare	Reimchen 1994, Nagorsen et al. 1989, 1991, Hatler 1976	British Columbia
Striped Skunk	Rare	Cederholm et al. 1989	Washington
Long-tailed Weasel	Rare	Cederholm et al. 1989	Washington