Pacific Salmon Carcasses:

Essential Contributions of Nutrients and Energy for Aquatic and Terrestrial Ecosystems

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ABSTRACT

Pacific salmon and other anadromous salmonids represent a major vector for transporting marine nutrients across ecosystem boundaries (i.e., from marine to freshwater and terrestrial ecosystems). Salmon carcasses provide nutrients and energy to biota within aquatic and terrestrial ecosystems through various pathways. In this paper we review and synthesize the growing number of studies documenting this process in different localities. We also discuss the implications for maintaining the nutrient feedback system. Our findings show that future management will need to view spawning salmon and their carcasses as important habitat components for sustaining the production of fish as well as other salmon-dependent species within watersheds.

Pacific salmon and other salmonids (*Oncorhynchus* spp.) have evolved several unique adaptations to survive and exploit resources in a wide range of aquatic environments, including freshwater, estuarine, and marine ecosystems (Neave 1958; Foerster 1968; Miller and Brannon 1981). Of central significance are the behaviors of *anadromy* (fishes that spend most of their lives in the ocean and migrate to freshwater to breed) and *semelparity* (dying after spawning once). Many species have adopted these behaviors, including chinook (*O. tshawytscha*), chum (*O. keta*), pink (*O. gorbuscha*), sockeye (*O. nerka*), coho (*O. kisutch*), masu (*O. masou*), and amago (*O. rhodurus*) (see Groot and Margolis 1991). Anadromous trout such as cutthroat (*O. clarki*) and steelhead (*O. mykiss*) repeatedly spawn (*iteroparity*) to varying degrees, depending on individual runs (Miller and Brannon 1981).

Since most species of *Oncorhynchus* are semelparous, a healthy spawning run will produce a large number of carcasses after the fish have spawned. Scientists have long observed that these carcasses play an important role in providing food for terrestrial consumers, as Russian expeditioner V. K. Arseniev observed around 1906 along one of the rivers emptying into the Sea of Japan:

> *For cleaning up these swarms of fish nature sent sanitary officials in the form of bears, pigs, foxes, badgers, raccoon, dogs, crows...and jays. The dead fish were taken by the birds as a rule, while the mammals tried to catch the living ones* (Arseniev 1941:196, reprinted 1996).

Pacific salmon also have been considered important vectors for returning significant amounts of nutrients from the northern Pacific Ocean back to land, representing a unique way to move nutrients upstream. This subject has attracted attention from scientists and economists throughout the Pacific Rim. Consider Japan's Edo era (1603–1867), when people believed that a streamside forest could provide fish with numerous benefits such as cover, nutrients, and food. This belief remained in the minds of people living near waterfronts or forests after the Meiji Restoration (1868). When the first forest act of Japan was introduced at the beginning of the twentieth century, it contained an article ordering conservation of *uo-tsuki-rin*, literally "fish-attracting forest." Using anecdotal information, Sibatani (1996) suggested that uo-tsuki-rin may operate in the opposite direction: "The land near rivers is well fertilized by the ocean nutrients brought by ascending (spawning) salmon, which causes the forests to thrive."

The movement of marine nutrients inland can be considered in the context of the Native American culture in the Pacific Northwest, too. Many Native American tribes in the Columbia River basin traveled long distances to partake in the catch and consumption of salmon, and in doing so distributed their excrement over this vast watershed and beyond. Some tribes of the upper Columbia were known even to cross the Continental Divide to trade dried fish with tribes of the upper Missouri River basin (NPPC 1986), thus providing an additional mechanism for transferring marine-derived nutrients to the surrounding land mass.

Accumulating research now suggests that Pacific salmon carcasses can supply marine nutrients to both aquatic and terrestrial ecosystems, thereby having the

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potential to influence the structure and function of some stream systems and wildlife communities. Since salmon adults spend long periods feeding in the ocean and generally do not feed once they enter freshwater to spawn, the nutrients they release are almost entirely of marine origin (Krokhin 1975; Mathisen et al. 1988; Kline et al. 1993). This process represents a major link among marine, freshwater, and terrestrial ecosystems since salmon can be important vectors for moving significant amounts of nutrients across ecosystem boundaries.

This knowledge has enormous implications for ecosystem management and the maintenance of other nutrient cycles in general (Sibatani 1996; Tsuchida 1996; Murota 1998). Responsible management will need to recognize the top-down effects (Northcote 1988) of spawning salmon on aquatic and terrestrial ecosystems. This will mean shifting emphasis to accept spawning salmon and their carcasses as important habitat components for sustaining the production of fish as well as other salmon-dependent species within watersheds.

This paper reviews and synthesizes the literature on studies of nutrient subsidy provided by salmonid carcasses and their effects on aquatic environments and vertebrate communities. We also explore the implications for maintaining the nutrient feedback system.

The return of nutrients by anadromous fish: evidence from research

Several studies have quantified the process of anadromous and semelparous fishes returning ocean nutrients to their spawning areas. These studies have involved research methods ranging from direct observation and photography to the use of stable isotope tracers and mass spectrometry. The accuracy of the latter methods has allowed for direct and quantitative evidence of the flow of nutrients from spawning salmon into freshwater trophic systems.

The literature suggests that the fate and utilization of nutrients provided by decomposing salmon carcasses may depend on numerous variables, including species (spawning densities and location in the watershed preferred for spawning), in-stream physical structure (retention of organic debris or otherwise), discharge (high stream flows), biotic mechanisms (consumption by aquatic and terrestrial invertebrates, fish, and terrestrial wildlife), and riparian ecosystem conditions (the amount of light that limits primary productivity). Comparing and contrasting studies will illustrate how these variables lead to differences in nutrient use.

The majority of studies show that primary production in lakes and streams is increased by nutrients released by salmon carcasses. Early studies with lakes in Alaska focused on nutrient return by large runs of sockeye salmon. Salmon carcasses contributed nitrogen and phosphorous compounds to lakes and their tributaries, which probably enhanced the supply of phytoplankton and zooplankton available for young sockeye salmon during their two- to four-year residence in the lakes (Juday et al. 1932; Donaldson 1967). These early studies showed that salmon carcasses provided a feedback loop that sustained the progeny of adult spawners.

In more-advanced lake studies, Mathisen et al. (1988) and Kline et al. (1993) investigated the fate of nutrients released by salmon carcasses in Kvichak River/Iliamna Lake, Alaska, using stable isotopes. Stable isotope tracers such as ^{13}C and ^{15}N trace nitrogen and carbon from spawning salmon through the trophic systems of lakes and streams the fish use (Mathisen et al. 1988; Kline et al. 1990; Bilby et al. 1996). This is because N and C in spawning salmon contain higher proportions of the heavier isotopic form than N and C imported into streams from other sources (Kline et al. 1990). Use of the tracers makes it possible to determine what percentage of N and C is marine-derived.

Mathisen et al. (1988) verified that marine nutrients, especially nitrogen, are traceable to different trophic levels and enhance system fertility. Samples for the stable N isotope analysis were collected from periphyton, plankton, sediments, and resident fish species in the Iliamna Lake system where salmon spawned. The scientists found a higher ^{15}N percentage in the samples collected than in the nearby control system, indicating that marine-derived nutrients had been incorporated into the biota of Iliamna Lake. Mathisen et al. (1988) suggested that periphyton used the nutrients first, which then supported populations of resident fishes. Adult salmon excretion and gamete release prior to death also contributed substantial amounts of marine nitrogen (approximately 30% of the total) and other biogenic nutrients after the fish had been in freshwater for more than a month.

In a more extensive study in the same area, Kline et al. (1993) compared $^{15}N/^{14}N$ in food webs of systems with anadromous salmon and those without. Their results also revealed that the biota of Iliamna Lake had higher stable isotope ratios of ^{15}N than biota in control

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Spawning salmon provide a period of high food abundance to other animals such as eagles or mink.

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Live and dead chum salmon spawners lie in a small tributary of Kennedy Creek near Olympia, Washington.

lakes. The researchers suggested that the primary pathway of marine-derived nitrogen into biota was not through direct consumption of eggs and fry, but *remineralization*, or uptake by primary producers. This supports the ideas of Juday et al. (1932), Donaldson (1967), and Mathisen et al. (1988) that primary production is an important means of uptake of nutrients released by carcasses in lake systems.

In contrast, Gross et al. (1998) used a simulation model for Redfish Lake, Idaho, to predict that marine-derived nutrients from sockeye salmon were not of major importance to lake production. The simulation model suggested that marine-derived nutrients accounted for only 3% of the annual phosphorous load of the lake, even before hydropower dams were present on the Snake River. The authors suggested that low smolt-to-adult survival rates, rapid flushing, and phosphorous export by smolts contributed to the system's low level of dependence on marine-derived nutrients from sockeye salmon.

Studies also have shown differences in how nutrients from salmon carcasses affect primary production in stream systems. Studies have found primary production to be the sole (Richey et al. 1975) or partial (Kline et al. 1990; Piorkowski 1995; Shuldt and Hershey 1995) pathway by which salmon-derived nutrients are used by food webs in streams. For example, Richey et al. (1975) studied nonanadromous sockeye salmon (kokanee) carcasses in Taylor Creek, a tributary to Lake Tahoe, California, and found they significantly affected the primary production of the creek. The authors studied two seasons, one of high spawner abundance and one of low spawner abundance with a severe flood event that flushed the stream of carcasses. During the season of high spawner abundance, they found that the carcasses stimulated bacterial and fungal activity, leading to the release of nitrate, phosphate, and eventually a bloom of phytoplankton and periphyton. This supports the assumption that spawner abundance can determine the ultimate amount of nutrients released. Richey et al. (1975) found that 44.6 kg of phosphorous were introduced in the larger run as opposed to 17.3 kg in the smaller run. Presumably, the winter freshet associated with the smaller kokanee run affected the amount of nutrients made available for use in the spawning reach.

Other stream studies have found no significant increase in primary productivity after salmon spawned or when carcasses were experimentally introduced (Minshall et al. 1991; Rand et al. 1992). Minshall (1991) studied nonanadromous rainbow trout carcasses in Mink Creek, Idaho, and found that nutrient uptake was restricted to microheterotrophs directly associated with the carcasses or direct ingestion by invertebrate consumers. The authors suggested that tight nutrient spirals and high nutrient retention limited primary production. Rand et al. (1992) found that coho and chinook salmon carcasses in two Lake Ontario tributaries did not account for a significant increase in phosphorous discharged from their study streams. The authors conclude that salmon carcasses are unlikely to affect primary production in this area due to naturally high concentrations of phosphorous. Also, western streams may export less total phosphorous during an annual cycle than eastern streams, as seen when the total phosphorous value of Donaldson (1967) is compared to Rand et al. (1992) (8.0 ug$\cdot$L^{-1} versus 24.0 ug$\cdot$L^{-1}, respectively).

Some studies have suggested that pathways other than autotrophic uptake are responsible for the incorporation of marine-derived nutrients into the trophic systems of streams. Bilby et al. (1996) used stable isotopes to investigate the incorporation of nitrogen and carbon from coho salmon into the trophic systems of two tributaries of the Snoqualmie River in Washington. Primary production in the study streams was limited due to low levels of light, short day lengths, cold temperatures, and frequent scouring flows at the time salmon carcasses were present. Other than direct consumption of carcasses, eggs, and emerging fry by fish and some invertebrates, incorporation of nutrients occurred while N and C were in an organic form, prior to mineralization. Laboratory experiments revealed that dissolved Kjeldaul-N derived from carcasses was rapidly removed from solution by the streambed gravel, even in the absence of light. This pathway for use of nutrients by stream biota occurred through uptake of dissolved organic matter released by decomposing carcasses by microfauna in the streambed substrate.

A third pathway for use of nutrients released by salmon carcasses in aquatic systems occurs through direct consumption of salmon eggs, fry, and carcasses. Many studies have used stable isotope tracers to find evidence of incorporation of marine-derived nutrients in biota within streams.

Kline et al. (1990) compared the 15N of biota from a section of Sashin Creek in Alaska that supported pink salmon and another section upstream of a 30-m waterfall where salmon had no access. Values of 15N and 13C between the two sections were isotopically distinct, indicating that the spawning section was enriched by marine nutrients transported by adult pink salmon. Since juvenile pink salmon have a brief freshwater residence, Kline et al. (1990) speculated that other resident fish species of the creek may have been the primary benefactors of nutrients provided by the spawning run. However, nutrient uptake in the nearby estuary may benefit pink salmon (Brickell and Goering 1970). This pathway has received limited investigation, although it is logical to assume that some estuarine systems receive significant inputs of salmon-derived nutrients when carcasses are flushed from streams during high flows. In support of this hypothesis, Fujiwara and Highsmith (1997) found elevated nitrogen stable isotope ratios of *Ulva* sp., an estuarine macroalga, after a salmon run in Seldovia Bay, Alaska. The authors suggested that a nutrient link exists between adult and juvenile chum salmon in the estuary because juvenile salmon feed on harpacticoid copepods, organisms dependent on *Ulva* sp. In addition, Reimchen (1994) found 10 species of marine invertebrates associated with salmon carcasses in the Bag Harbour estuary of Gwaii Haanas, British Columbia. These scavengers included starfish, shrimp, and crabs.

Bilby et al. (1996) compared N and C isotope ratios among several aquatic organisms collected from two streams that supported coho salmon and two streams that had impassable waterfalls. The researchers found that ^{15}N and ^{13}C values of the biota were significantly greater at anadromous sites, particularly after carcasses had fully decomposed. Bilby et al. (1996) found that epilithic organic matter and fish were significantly enriched with ^{15}N and ^{13}C. For example, average contribution of N ranged from 11% for invertebrate predators to 31% for juvenile coho salmon, and salmon-derived C ranged from 25% for epilithic organic matter to 40% for juvenile coho. The highest percentage of N in the biota was 46% for adult cutthroat trout and 61% C for age-1-plus steelhead.

Bilby et al. (1996) also monitored growth rates of juvenile fish, finding that age-0-plus coho salmon exhibited a doubling in growth rate after adults spawned in the stream. In a nearby stream without spawning salmon, age-0-plus steelhead showed no change in growth rate during the winter. High growth rates can increase the overwinter survival rate, and larger smolt size has been related to increased marine survival (Bilton et al. 1982; Ward and Slaney 1988). Piorkowski (1995) also found that direct consumption of salmon biomass was the main avenue of nutrient uptake for salmon fry, grayling (*Thymallus* spp.), and rainbow trout (*O. mykiss*) in southcentral Alaskan streams.

Contributions of marine nutrients from salmon eggs could be significant in many stream systems since an average of only 10%–30% of eggs deposited by a female will survive to emerge as fry (Koski 1966, 1975; Tagart 1976). Many birds (Mossman 1958; Moyle 1966; Reimchen 1994), fishes (Armstrong 1970; Eastman 1996), aquatic insects (Nicola 1966; Ellis 1970), and even mammals (Moyle 1966; Reimchen 1994; see Willson and Halupka 1995) will readily consume salmon eggs, either through direct predation of or scavenging in redds, or by feeding on eggs that have become dislodged by subsequent spawning activities or storm events.

Macroinvertebrate communities in streams receiving salmon runs can change in response to spawning activity and nutrient enrichment. In two tributaries to the Snoqualmie River, and in Kennedy Creek, both in Washington, Minakawa (1997) found that aquatic insect abundance was temporarily reduced due to spawning activity. However, the subsequent presence of salmon carcasses produced a two-fold or greater increase in total insect densities and biomass compared to control reaches. Piorkowski (1995) found insect taxa richness and diversity increased 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. (1996) found all functional feeding groups except shredders to be enriched with ^{15}N and ^{13}C in western Washington streams after coho salmon spawning. In streams near Lake Superior, Schuldt and Hershey (1995) concluded that salmon-derived nitrogen was incorporated into grazing mayflies and filter-feeding caddisflies (*Hydropsyche* spp.), although the overall use of carcasses by invertebrates was low. Wipfli et al. (1998) also report macroinvertebrate densities 8–25 times higher in carcass-enriched areas of artificial and natural streams in southeast Alaska. Johnston et al. (1997) found that at sites in interior British Columbia with high salmon abundance (0.6–2.6 salmon per m^{-1}), up to 60% of the nitrogen content of benthic insects was derived from salmon tissue. Increases in the abundance and biomass of macroinvertebrates could potentially provide more food for resident and overwintering juvenile fish as well as other biota within the riparian ecosystem (Wipfli et al. 1998).

Many studies have suggested that other variables influence the use of nutrients released by salmon carcasses. Donaldson (1967) found that the quantity of nutrients introduced into freshwater systems was related to how many adults return to spawn. Consequently, different


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Small organic debris helps retain chum salmon carcasses in Kennedy Creek.


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Salmon carcasses often affect many production levels in stream ecosystems.

species of salmon may contribute varying amounts of nutrients based on their intrinsic spawning densities and biomasses. Sockeye salmon typically spawn in high numbers, as do pink and chum salmon. More-dispersed spawning species such as coho salmon may transport fewer overall nutrients during a spawning run, although their nutrient subsidy is significant, particularly in the smaller streams they tend to use. Anadromous trout such as cutthroat and steelhead can repeatedly provide nutrients and energy to aquatic and terrestrial systems, at least through egg deposition, since up to 30% may live through their first spawning (Stolz and Schnell 1991). Evidence also exists that certain terrestrial insects, as shown by their maggots, will colonize carcasses rapidly and consume a significant amount of salmon biomass (Reimchen 1994).

Current velocity and the presence and effectiveness of physical retention devices influence the ability of a stream to retain carcasses and may, therefore, influence how or where nutrients are used. For example, Cederholm and Peterson (1985) found that organic debris played a significant role in retaining coho carcasses in streams on the Olympic Peninsula of Washington. When 20 marked carcasses were placed in 9 streams, researchers found 80% of them remained in the first 200 m downstream of release sites after 7 days, and streams with more organic debris retained more carcasses. Cederholm et al. (1989) verified these results when 920 coho carcasses were released in 7 streams on the Olympic Peninsula. Organic debris retained most of the carcasses within 100 m of release, even during floods. Piorkowski (1995) also found carcasses were retained by organic debris in several southcentral Alaskan streams, although some streams retained carcasses even when organic debris biomass was low. Piorkowski (1995) suggests that low stream flow and the behavior of salmon to seek shallow, slow-moving backwaters before death helps streams retain carcasses.

Spawning locations in the watershed of different salmon species may influence the use of released nutrients. Brickell and Goering (1970) found that after spawning and dying in Sashin Creek, most pink salmon were flushed to the Little Port Walter estuary of Alaska. Increases of dissolved organic nitrogen occurred in both Sashin Creek and the Little Port Walter Estuary; a nearby control estuary that did not support a salmon run did not show increased dissolved organic nitrogen. Sediment samples in the estuary were gelatinous, presumably from accumulated pink salmon carcasses. Pink salmon spawn in the lower reaches of watersheds, whereas coho tend to migrate much further upstream to spawn in smaller streams that likely contain organic matter (Vannote et al. 1980). However, the results of Kline et al. (1990) suggested that biota in Sashin Creek was enriched with marine-derived nitrogen from spawning pink salmon. In this case, the high spawning density of a particular species may offset a stream's ability to retain carcasses, especially in the absence of flood events. Also, biotic retention mechanisms such as feeding macroinvertebrates and fish can contribute to carcass disintegration and facilitate the use of nutrients within a spawning reach in the absence of physical retention devices (Piorkowski 1995).

In summary, marine-derived nutrients can be released to freshwater systems by anadromous fishes through excretion, gametes, or their own mortality. Although differences can occur from locality to locality, the pathways for use of nutrients by stream biota seem to occur through three avenues: (1) uptake by primary producers after mineralization to inorganic forms that then transfer the nutrients up the food chain; (2) uptake of dissolved organic matter released by decomposing carcasses by microfauna in the streambed substrate; and (3) direct consumption of salmon eggs, fry, and carcasses. Variables for utilization seem to include differences among salmonid species, including spawning densities and location preferred for spawning in a watershed. Hydrologic discharge, the ability of a stream system to retain carcasses through physical and biotic mechanisms, and riparian ecosystem conditions that influence autotrophic productivity also seem to be important variables. In addition, it is important to consider the ratio of nutrients leaving a system (i.e., smolts migrating to the ocean) to those brought back by returning adult salmon. Spawning salmon provide marine-derived nutrients to aquatic ecosystems, and these contribute to biological productivity through many pathways (See Figure 1).

Importance of salmon carcasses as nutrients and energy for terrestrial ecosystems

Salmon carcasses can supply a critical source of energy for some terrestrial vertebrates and provide nutrients for riparian vegetation along some spawning streams. Although the pathways of marine-derived nutrients into and throughout terrestrial trophic systems have not been as quantitatively documented relative to aquatic systems, recognition of salmon as a "keystone" species in vertebrate communities is warranted (Willson and Halupka 1995).

Accumulating evidence indicates that many animals' reproductive cycles and seasonal distribution are tied directly to a spawning run of salmon. Hunt et al. (1992) found that the number of bald eagles (*Haliaeetus leucocephalus*) wintering along the Skagit River in Washington was correlated with chum salmon escapement. Eagle numbers were inversely associated with high stream flows and flood events when carcasses were removed from gravel bars. Coho salmon carcasses in tributaries were a major food source later in winter after chum carcasses had been consumed or flushed from the mainstem. Numerous other studies have documented a similar correlation between the availability of spawning salmon and eagle distribution and reproductive success (McClelland et al. 1982; Stalmaster and Gessamen 1984; Hansen 1987).

Ben-David (1997) found that timing of reproduction in female mink *(Mustela vison)* of Chichagof Island, Alaska, shifted to coincide with the availability of salmon carcasses. Annual runs of coho, chinook, and pink salmon provide female mink with unlimited food supplies, helping to meet the nutritional requirements of lactation. Spawning salmon provide animals' young with a period of high food abundance, giving them a selective advantage for survival.

Many of the energy requirements for hibernation in some bears are met by consuming salmon carcasses (see Willson and Halupka 1995). This is because salmon are more nutrient-dense than virtually any other food source available to bears along the Pacific Northwest coast (Hilderbrand et al. 1996). Hilderbrand et al. (1996) used stable isotopes to determine that salmon contributed 33%–90% of the metabolized carbon and nitrogen in grizzly bears (*Ursus arctos horribilis*) in the Columbia River basin of the Pacific Northwest prior to 1931. Coastal Alaskan brown bears obtain virtually all of their carbon and nitrogen from salmon (94% ± 9% of total) (Hilderbrand et al. 1996). Continued research with stable isotope analysis should lead to further understanding of the complex trophic interactions and pathways of salmon-derived N and C into terrestrial animals.

The animals using salmon carcasses within a riparian ecosystem each feed on various parts of the carcass. According to Cederholm et al. (1989), 22 species of mammals and birds were observed or known to consume salmon carcasses in 7 streams of the Olympic Peninsula, Washington (see also a review by Willson and Halupka 1995). Large carnivores such as bears or eagles will first kill live salmon or retrieve carcasses from pools and then carry the carcass to the adjacent bank to be wholly or partially consumed (Moyle 1966; Cederholm et al. 1989; Reimchen 1994). Smaller animals and scavengers then concentrate on the remainder of the carcass until just bone matter remains. Some small mammals may even use bone material from carcasses deposited on stream banks (Cederholm et al. 1989).

Terrestrial wildlife may benefit indirectly from a food source in the aquatic system that has been enriched by nutrients provided by salmon carcasses, although this has not been quantitatively documented. The increase in aquatic macroinvertebrate biomass and taxonomic richness associated with the presence of salmon carcasses (Piorkowski 1995; Minakawa 1997; Wipfli et al. 1998) could potentially provide more food to support wildlife populations in watersheds. Similar interactions are presumably present with the increase in growth rate of juvenile fish since certain birds (Wood 1987*a*, *b*) and mammals (Dolloff 1993) will capitalize on juvenile salmonids as a food source (see also Willson and Halupka 1995).

Bears, and presumably other large mammals and birds, can transport carcasses anywhere from 5 m to 200 m from streambanks (Shuman 1950; Cederholm et al. 1989; Reimchen 1994) and often will not consume carcasses in the same location (Reimchen 1994; Piorkowski 1995). The number of carcasses transported from a stream channel to riparian forest can constitute a large percentage of a stream's total salmon run; Reimchen (1994) estimated that 3,611 carcasses, or 63% of an entire run, were transferred to the riparian ecosystem by 3–8 black bears (*U. americanus*) in a stream in Gwaii Haanas, British Columbia. This allows for random distribution of salmon biomass and salmon-derived nutrients, and could have a fertilizing effect on riparian vegetation. Fertilization could occur either through the direct deposition of a carcass or through fecal matter of animals that have consumed carcasses. Bilby et al. (1996) found that foliage of riparian vegetation along a salmon stream contained 18% marine-derived nitrogen. Piorkowski (1995) also found that terrestrial

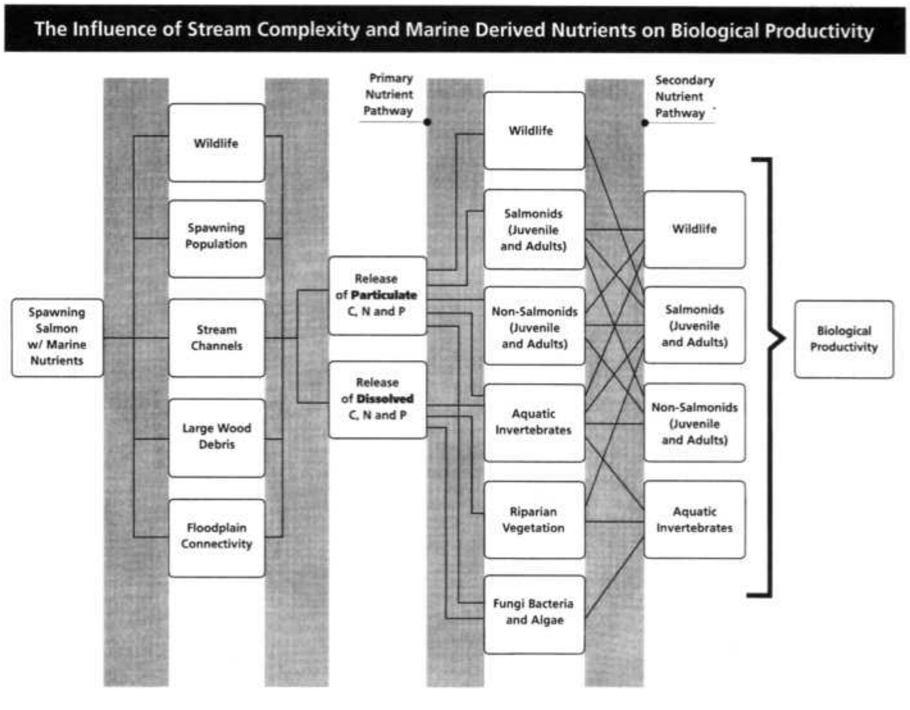

Figure 1. The influence of spawning salmon and marine-derived nutrients on biological productivity.

vegetation along selected streams in Alaska was enriched with marine-derived nitrogen. These results illustrate the need to further investigate the influence of salmon-derived nutrients on riparian vegetation of different sizes and types of streams.

Anadromous salmon and their carcasses clearly have significant roles in providing food and nutritive resources to numerous terrestrial animals. The presence and availability of salmon during fall and winter may be of special utility to many animals since other food sources are limited at that time. Willson and Halupka (1995) speculated that if a stream loses its anadromous salmon population, the spatial distribution of wildlife consumers, their nutritional status, and their reproductive success are likely to be altered. Therefore, the ecologically significant linkages between anadromous salmon and terrestrial wildlife merits increased attention in fish and wildlife management, ecosystem-based management plans, and ecological research (Willson and Halupka 1995).


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Fly maggots facilitate decomposition of salmon carcasses.

Maintaining the salmon nutrient feedback system

As the decline of indigenous wild salmon continues throughout Washington, Oregon, Idaho, California (Nehlsen et al. 1991), and elsewhere, it is logical to assume that the productivity of some freshwater and terrestrial ecosystems will be diminished because of reduced nutrients and biomass returned from the ocean. The impact of this nutrient deficit to the largest river basins in the North Pacific is difficult to quantify but deserves consideration. For example, the Russian Federation's 4,440-km-long Amur River and its additional 6,000 km of tributaries contain approximately 100 species of fish, many of which are anadromous. Sibatani (1996) used early records of Japanese fisheries that operated around 1910 at Nikolaiyevsk, situated at the mouth of the Amur, where the seabed was allegedly "carpeted with fishes." He estimated that at least 20 million salmon once entered the Amur and its tributaries each year, enriching the watershed with inorganic nutrient salts derived from the marine environment, whereas the current salmon population has drastically diminished in the Russian Far East, especially along the coast of the Sea of Japan.

The once-abundant salmon runs of the Columbia River provide another example. Before Europeans settled the Pacific Northwest, salmon had access to more than 20,000 km of main river and tributaries (NPPC 1986). According to the NPPC (1986), the estimated total annual Columbia River salmon and steelhead run size was 9.6 million–16.3 million fish. With an average salmon weight of 6.75 kg each, this amounted to a conservative estimate of more than 67,700 mt of salmon returning to the river each year. Of this total weight of salmon, scientists estimated (NPPC 1986) that tribal groups annually caught 18,960 mt, leaving up to 45,150 mt of salmon spawners and eventual contributors to the broader fish and wildlife ecosystem. The current runs in the Columbia River total less than 2 million adults, and most of these are hatchery-produced fish that either will be caught in fisheries or will return to the hatchery of their origin (Bisson and Bilby 1998). A preliminary estimate of the 1997 Columbia River basin natural salmon spawning escapement (wild plus stray hatchery fish) would be approximately 0.5 million fish (Pacific Fishery Management Council 1998). Using the same average weight per fish as above, this would amount to approximately 3,400 mt of carcasses.

Decreased production could be self-perpetuating since stocks already in decline are likely to decrease further (Bilby et al. 1996; Larkin and Slaney 1997). The impending listing of many salmon stocks as endangered or threatened has forced federal and state government agencies to aggressively act to protect and recover salmon (WDFW 1997). The numerous ecological effects of spawning salmon should be important components of recovery plans for salmon and their ecosystems.

Considering the research that has documented the importance of anadromous salmon for watershed ecosystem health, there are numerous implications for management of fisheries and stream and riparian ecosystems. An obvious scenario includes allowing sufficient salmon to spawn in all waterbodies historically used within a watershed. A diversity of species that use several stream orders will distribute marine nutrients and energy throughout entire stream systems and adjacent upland ecosystems.

Ecosystem health will presumably benefit from having the largest number of spawners possible (WDFW 1997), which in turn would produce a large number of carcasses. Escapement goals should be designed to build "nutrient capital" within watersheds (Bilby et al. 1996; Larkin and Slaney 1997) that will help support the next generation of fish. Research is underway to establish the number of carcasses and corresponding nutrients needed to maintain productive rearing salmonid populations in streams and lakes (Michael 1998; Schmidt et al. 1998), and researchers also should examine the density-dependent mortality implications of increased escapement. To sustain all salmon-dependent biota, further research should focus on nutrient levels and carcass biomass needed to maintain other ecosystem components such as terrestrial wildlife.

Management that considers interspecies interactions and effects should be more beneficial to overall fish production (Michael 1995). For example, nutrient influx from pink salmon runs can influence the recruit-per-spawner, smolt size and number, and ocean survival of other rearing salmonids (Ward and Slaney 1988; Michael 1995). While linkages between anadromous fish and certain threatened wildlife species (i.e., grizzly bears) are considered, the recovery of salmon populations can enhance and facilitate the recovery of other salmon-dependent species (Hilderbrand et al. 1996).

Forests and their riparian ecosystems need to be managed to provide organic debris recruitment for stream channels. In addition to numerous habitat and morphological functions (Bisson et al. 1987), organic debris will help retain carcasses in streams for biological activity. The capacity of many small streams to retain carcasses has probably been reduced by human activities (Cederholm et al. 1989). This could seriously affect the food supply of some carnivore wildlife species, particularly in small streams where organic debris loading is generally at high levels under undisturbed conditions.

Hatchery salmon carcasses may be valuable in streams where wild spawners are lacking, although they should not be considered a long-term solution to replacing the nutrient subsidy of wild salmon. Many dying wild salmon seek shallow backwaters and small, remote headwater tributaries, making carcasses more accessible to terrestrial carnivores (Cederholm et al. 1989; Piorkowski 1995). There may be potential for disease transfer if carcasses are moved outside local drainages (Larkin and Slaney 1997). Furthermore, the physical act of spawning displaces fine sediments from spawning riffles, improving spawning conditions for adults arriving later in the run (Peterson and Quinn 1994). However, placement of hatchery salmon carcasses has been documented to increase the densities of age-0-plus coho salmon and age-0-plus and age-1-plus steelhead in small southwestern Washington streams (Bilby et al. 1998). Further research and monitoring with hatchery carcass placement in different salmon streams will help managers determine the applicability of this type of enhancement practice.

To ensure effective recycling of nutrients from the ocean back to land, the major vector of this process—wild anadromous salmonids—must recover from its current status. Identifying and securing channels for recycling inorganic nutrients are important components of biological diversity maintenance, at least in the North Pacific (Sibatani 1996; Murota 1998). The key to sustaining the human economy also may lie in these material cycles to some degree since our economy relies heavily on healthy ecosystems to sustain food production and other resources (see Murota 1987; Tsuchida 1996; Murota 1998). Therefore, the importance of the nutrient feedback system of anadromous Pacific salmon illustrates the need for continued research and corresponding management to protect and recover native salmonid populations before the system collapses entirely.

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References

Armstrong, R. H. 1970. Age, food, and migration of Dolly Varden smolts in Southeastern Alaska. J. Fish. Res. Bd. Can. 27:991–1,004.

Arseniev, V. K. (Translation by M. Burr). 1996. Dersu the trapper. (Field observations made in 1906). Copyright 1941 by E. P. Dutton & Co., Inc., renewed 1968. Reprinted by arrangement with Dutton Signet, a division of Penguin Books USA Inc. McPherson and Co., Kingston, New York.

Ben-David, M. 1997. Timing of reproduction in wild mink: the influence of spawning Pacific salmon. Can. J. Zool. 75:376–382.

Bilby, R. E., B. R. Fransen, and **P. A. Bisson.** 1996. Incorporation of nitrogen and carbon from spawning coho salmon into the trophic system of small streams: evidence from stable isotopes. Can. J. Fish. Aquat. Sci. 53:164–173.

Bilby, R. E., B. R. Fransen, P. A. Bisson, and **J. K. Walter.** 1998. Response of juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead (*Oncorhynchus mykiss*) to the addition of salmon carcasses to two streams in southwestern Washington, U.S.A. Can. J. Fish. Aquat. Sci. 55:1,909–1,918.

Bilton, H. T., D. F. Alderice, and **J. T. Schnute.** 1982. Influence of time and size at release of juvenile coho salmon (*Oncorhynchus kisutch*) on returns at maturity. Can. J. Fish. Aquat. Sci. 39:426–447.

Bisson, P. A., R. E. Bilby, M. D. Bryant, C. A. Dolloff, G. B. Grette, R. A. House, M. L. Murphy, K. V. Koski, and **J. R. Sedell.** 1987. Large woody debris in forested streams in the Pacific Northwest: past, present, and future. Pages 143–190 *in* E. O. Salo and T. W. Cundy, eds. Streamside management: forestry and fishery interactions. College of Forest Resources, University of Washington, Seattle.

Bisson, P. A., and **R. E. Bilby.** 1998. Organic matter and trophic dynamics. Pages 373–398 *in* R. J. Naiman and R. E. Bilby, eds. River ecology and management: lessons from the Pacific coastal ecoregion. Springer-Verlag, New York.

Brickell, D. C., and **J. J. Goering.** 1970. Chemical effects of salmon decomposition on aquatic ecosystems. Pages 125–138 *in* R. S. Murphy, ed. First International Symposium on Water Pollution in Cold Climates. U.S. Government Printing Office, Washington, DC.

Cederholm, C. J., and **N. P. Peterson.** 1985. The retention of coho salmon (*Oncorhynchus kisutch*) carcasses by organic debris in small streams. Can. J. Fish. Aquat. Sci. 42:1,222–1,225.

Cederholm, C. J., D. B. Houston, D. L. Cole, and **W. J. Scarlett.** 1989. Fate of coho salmon (*Oncorhynchus kisutch*) carcasses in spawning streams. Can. J. Fish. Aquat. Sci. 46:1,347–1,355.

Dolloff, C. A. 1993. Predation by river otter (*Lutra canadensis*) on juvenile coho salmon (*Oncorhynchus kisutch*) and Dolly Varden (*Salvelinus malma*) in southeast Alaska. Can. J. Fish. Aquat. Sci. 50:312–315.

Donaldson, J. R. 1967. The phosphorus budget of Iliamma Lake, Alaska, as related to the cyclic abundance of sockeye salmon. Ph.D. dissertation. University of Washington, Seattle.

Eastman, D. E. 1996. Response of freshwater fish communities to spawning sockeye salmon (*Oncorhynchus nerka*). M.S. thesis. University of Washington, Seattle.

Ellis, R. J. 1970. Alloperla stonefly nymphs: predators or scavengers on salmon eggs and alevins? Trans. Am. Fish. Soc. 99:677–683.

Foerster, R. E. 1968. The sockeye salmon, *Oncorhynchus nerka*. Bull. Fish. Res. Board Can. 162:1–422.

Fujiwara, M., and **R. C. Highsmith.** 1997. Harpacticoid copepods: potential link between inbound adult salmon and outbound juvenile salmon. MEPS 158:205–216.

Gard, R. 1971. Brown bear predation on sockeye salmon at Karluk Lake, Alaska. J. Wildl. Manage. 35:193–204.

Groot, C., and **L. Margolis**, eds. 1991. Pacific salmon life histories. UBC Press, Vancouver, British Columbia, Canada.

Gross, H. P., **W. A. Wurtsbaugh**, and **C. Luecke.** 1998. The role of anadromous sockeye salmon in the nutrient loading and productivity of Redfish Lake, Idaho. Trans. Am. Fish. Soc. 127:1–18.

Hansen, A. J. 1987. Regulation of bald eagle reproductive rates in southeast Alaska. Ecology 68:1,387–1,392.

Hilderbrand, G. V., **S. D. Farley**, **C. T. Robbins**, **T. A. Hanley**, **K. Titus**, and **C. Servheen.** 1996. Use of stable isotopes to determine diets of living and extinct bears. Can. J. Zool. 74:2,080–2,088.

Hunt, G. V., **B. S. Johnson**, and **R. E. Jackman.** 1992. Carrying capacity for bald eagles wintering along a northwestern river. J. Raptor Res. 26:49–60.

Johnston, N. T., **J. S. Macdonald**, **K. J. Hall**, and **P. J. Tschaplinski.** 1997. A preliminary study of the role of sockeye salmon (*Oncorhynchus nerka*) carcasses as carbon and nitrogen sources for benthic insects and fishes in the 'Early Stuart' stock spawning streams, 1,050 km from the ocean. Fisheries project report no. RD55, Fisheries Branch, Ministry of Environment, Lands, and Parks, British Columbia, Canada.

Juday, C., **W. H. Rich**, **G. I. Kemmerer**, and **A. Mann.** 1932. Limnological studies of Karluk Lake, Alaska 1926–1930. Bull. Bur. Fish. 47:407–436.

Kline, T. C. Jr., **J. J. Goering**, **O. A. Mathisen**, **P. H. Poe**, and **P. L. Parker.** 1990. Recycling of elements transported upstream by runs of Pacific salmon: I. ^{15}N and ^{13}C evidence in Sashin Creek, southeastern Alaska. Can. J. Fish. Aquat. Sci. 47:136–144.

Kline, T. C. Jr., **J. J. Goering**, **O. A. Mathisen**, **P. H. Poe**, **P. L. Parker**, and **R. S. Scalan.** 1993. Recycling of elements transported upstream by runs of Pacific salmon: II. ^{15}N and ^{13}C evidence in the Kvichak River watershed, Bristol Bay, southwestern Alaska. Can. J. Fish. Aquat. Sci. 50:2,350–2,365.

Koski, K. V. 1966. The survival of coho salmon (*Oncorhynchus kisutch*) from egg deposition to emergence in three Oregon coastal streams. M.S. thesis. Oregon State University, Corvallis.

———. 1975. The survival and fitness of two stocks of chum salmon (*Oncorhynchus keta*) from egg deposition to emergence in a controlled-stream environment at Big Beef Creek. Ph.D. dissertation. University of Washington, Seattle.

Krokhin, E. M. 1975. Transport of nutrients by salmon migrating from the sea into lakes. Pages 153–166 *in* A.D. Hasler, ed. The coupling of land and water systems. Springer-Verlag, New York.

Larkin, G. A., and **P. A. Slaney.** 1997. Implications of trends in marine-derived nutrient influx to south coastal British Columbia salmonid production. Fisheries 22(11):16–24.

Mathisen, O. A., **P. L. Parker**, **J. J. Goering**, **T. C. Kline**, **P. H. Poe**, and **R. S. Scalan.** 1988. Recycling of marine elements transported into freshwater systems by anadromous salmon. Verh. Internat. Verein. Limnol. 23:2,249–2,258.

McClelland, B. R., **L. S. Young**, **D. S. Shea**, **P. T. McClelland**, **H. L. Allen**, and **E. B. Spettigue.** The bald eagle concentration in Glacier National Park, Montana: origin, growth, and variation in numbers. The Living Bird 19:133–155.

Michael, J. H., Jr. 1995. Enhancement effects of spawning pink salmon on stream rearing juvenile coho salmon: managing one resource to benefit another. NW Sci. 69:228–233.

———. 1998. Pacific salmon spawner escapement goals for the Skagit River watershed as determined by nutrient cycling considerations. NW Sci. 72:239–248.

Miller, R. J., and **E. L. Brannon.** 1981. Origin and development of life history patterns in Pacific salmonids. Pages 296–308 *in* E. L. Brannon and E. O. Salo, eds. Salmon and Trout Migratory Behavior Symposium. School of Fisheries, University of Washington, Seattle.

Minakawa, N. 1997. The dynamics of aquatic insect communities associated with salmon spawning. Ph.D. dissertation. University of Washington, Seattle.

Minshall, G. W., **E. Hitchcock**, and **J. R. Barnes.** 1991. Decomposition of rainbow trout (*Oncorhynchus mykiss*) carcasses in a forest stream inhabited only by nonanadromous fish populations. Can. J. Fish. Aquat. Sci. 48:191–195.

Mossman, A. S. 1958. Selective predation of glaucous-winged gulls upon adult red salmon. Ecology 39:482–486.

Moyle, P. 1966. Feeding behavior of the glaucous-winged gull on an Alaskan salmon stream. Wilson Bulletin 78:175–190.

Murota, T. 1987. The environmental economics of the water planet earth. Pages 185–199 *in* G. Pilet and T. Murota, eds. Environmental economics: the analysis of a major interface. R. Leimgruber, Geneva, Switzerland.

———. 1998. Material cycle and sustainable economy. Pages 120–138 *in* D. Bell, L. Fawcett, R. Keil, and P. Penz, eds. Political ecology. Routledge, London-New York.

Neave, F. 1958. The origin and speciation of *Oncorhynchus*. Trans. Roy. Soc. Can. 52:25–39.

Nehlsen, W., **J. E. Williams**, and **J. A. Lichatowich.** 1991. Pacific salmon at the crossroads: stocks at risk from California, Oregon, Idaho, and Washington. Fisheries 16(2):4–21.

Nicola, S. J. 1966. The relationship of Alloperla nymphs to incubating pink (*Oncorhynchus gorbuscha*) and chum (*Oncorhynchus keta*) salmon eggs, alevins, and pre-emergent fry in a southeastern Alaska stream. M.S. thesis. University of Washington, Seattle.

Northcote, T. G. 1988. Fish in the structure and function of freshwater ecosystems: a "top-down" view. Can. J. Fish. Aquat. Sci. 45:361–379.

NPPC (Northwest Power Planning Council). 1986. Council staff compilation of information on salmon and steelhead losses in the Columbia River basin. Columbia River Basin Fish and Wildlife Program, Portland, Oregon.

Pacific Fishery Management Council. 1998. Review of 1997 ocean salmon fisheries. National Oceanic and Atmospheric Administration, Award no. NA87FC0008. Portland, Oregon.

Peterson, N. P., and **T. P. Quinn.** 1994. Incubation environment of chum salmon (*Oncorhynchus keta*) in Kennedy Creek-Part A. Persistence of egg pocket architecture in chum salmon redds. Pages 9–25 *in* T. P. Quinn and N. P. Peterson, eds. The effects of forest practices on fish populations. Washington Department of Natural Resources and Cooperative Monitoring, Evaluation, and Research Committee. Timber/Fish/Wildlife, TFW-F4-94-001, Olympia, Washington.

Piorkowski, R. J. 1995. Ecological effects of spawning salmon on several southcentral Alaskan streams. Ph.D. dissertation. University of Alaska, Fairbanks.

Rand, P. S., C. A. S. Hall, W. H. McDowell, N. H. Ringler, and **J. G. Kennen.** 1992. Factors limiting primary productivity in Lake Ontario tributaries receiving salmon migrations. Can. J. Fish. Aquat. Sci. 49:2,377–2,385.

Reimchen, T. E. 1994. Further studies of predator and scavenger use of chum salmon in stream and estuarine habitats at Bag Harbour, Gwaii Haanas. Technical report prepared for Canadian Parks Service. Queen Charlotte City, British Columbia, Canada.

Richey, J. E., M. A. Perkins, and **C. R. Goldman.** 1975. Effects of kokanee salmon (*Oncorhynchus nerka*) decomposition on the ecology of a subalpine stream. J. Fish. Res. Board Can. 32:817–820.

Schmidt, D. C., S. R. Carlson, G. B. Kyle, and **B. P. Finney.** 1998. Influence of carcass-derived nutrients on sockeye salmon productivity of Karluk Lake, Alaska: importance in the assessment of an escapement goal. N. Am. J. Fish. Manage. 18:743–763.

Shuldt, J. A., and **A. E. Hershey.** 1995. Effect of salmon carcass decomposition on Lake Superior tributary streams. J. N. Am. Benthol. Soc. 14:259–268.

Shuman, R. F. 1950. Bear depredations on sockeye spawning populations in the Karluk River system, 1947. J. Wildl. Manage. 14:1–9.

Sibatani, A. 1996. (English translation by R. Davis). Why do salmon ascend rivers? Selected Papers on Entropy Studies 3:3–11.

Stalmaster, M. V., and **J. Gessmen.** 1984. Ecological energetics and foraging behavior of overwintering bald eagles. Ecol. Monogr. 54:407–428.

Stolz, J., and **J. Schnell.** 1991. Trout. Stackpole Books, Harrisburg, Pennsylvania.

Tagart, J. V. 1976. The survival from egg deposition to emergence of coho salmon in the Clearwater River, Jefferson County, Washington. M.S. thesis. University of Washington, Seattle.

Tsuchida, A. 1996. The importance of the 'cycle of matter': a discussion of nutrient cycling in basins, land, and human society from the viewpoint of entropy. Pages 150–170 *in* Clean Sea '96 International Workshop and Symposium on Environmental Restoration for Enclosed Seas. 27–30 August, Toyohashi, Japan.

Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, and **C. E. Cushing.** 1980. The river continuum concept. Can. J. Fish. Aquat. Sci. 37:130–137.

Ward, B. R., and **P. A. Slaney.** 1988. Life history and smolt-to-adult survival of Keogh River steelhead trout (*Salmo gairdneri*) and the relationship to smolt size. Can. J. Fish. Aquat. Sci. 45:1,110–1,122.

WDFW (Washington Department of Fish and Wildlife). 1997. Final environmental impact statement for the Wild Salmonid Policy. Washington Department of Fish and Wildlife, Olympia.

Willson, M. F., and **K. C. Halupka.** 1995. Anadromous fish as keystone species in vertebrate communities. Conserv. Biol. 9:489–497.

Wipfli, M. S., J. P. Hudson, and **J. P. Caouette.** 1998. Influence of salmon carcasses on stream productivity: response of biofilm and benthic macroinvertebrates in southeastern Alaska, U.S.A. Can. J. Fish. Aquat. Sci. 55:1,503–1,511.

Wood, C. C. 1987*a*. Predation of juvenile Pacific salmon by the common merganser (*Mergus merganser*) on eastern Vancouver Island. I: Predation during the seaward migration. Can. J. Fish. Aquat. Sci. 44:941–949.

———. 1987*b*. Predation of juvenile Pacific salmon by the common merganser (*Mergus merganser*) on eastern Vancouver Island. II: Predation of stream-resident juvenile salmon by Merganser broods. Can. J. Fish. Aquat. Sci. 44:950–959.