MINIREVIEW

Pacific Salmon, Nutrients, and the Dynamics of Freshwater and Riparian Ecosystems

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ABSTRACT

Pacific salmon (*Oncorhynchus* spp.) accumulate substantial nutrients in their bodies as they grow to adulthood at sea. These nutrients are carried to predominantly oligotrophic lakes and streams, where they are released during and after spawning. Research over more than 3 decades has shown that the annual deposition of salmon-borne marine-derived nutrients (MD-nutrients) is important for the productivity of freshwater communities throughout the Pacific coastal region. However, the pathways and mechanisms for MD-nutrient transfer and accumulation in freshwater and riparian ecosystems remain virtually unexplored, consequently, there are many uncertainties in this area. This article addresses three related topics. First, we summarize recent advances in our understanding of the linkages among MD-nutrients, freshwater (including riparian) ecosystems, and community dynamics by addressing the importance of MD-nutrients to lakes and streams and by then reviewing large-scale and long-term processes in the atmosphere and ocean that govern variability in salmon populations. Second, we evaluate the validity of the discoveries and their implications for active ecosystem management, noting areas where extrapolation from these results still requires great caution. Finally, we outline five key research issues where additional discoveries could greatly augment our understanding of the processes shaping the structure and dynamics of salmon populations and the characteristics of their freshwater habitat and associated riparian zones. Collectively, the data suggest that the freshwater portion of the salmon production system is intimately linked to the ocean. Moreover, for the system to be sustainable, a holistic approach to management will be required. This holistic approach will need to treat climate cycles, salmon, riparian vegetation, predators, and MD-nutrient flowpaths and feedbacks as an integrated system.

Key words: anadromous fishes; Pacific salmon; *Oncorhynchus*; marine nutrients; stable isotopes; lake; stream; riparian ecosystems; aquatic productivity; resource management.

INTRODUCTION

The role of Pacific salmon (*Oncorhynchus spp.*) in transferring nutrients between marine and freshwater environments has received considerable attention in the last decade (Willson and others 1998; Bilby and others 2001). The five species of Pacific salmon that perform this function utilize three unique life history traits—they are anadromous, they return to their natal streams to spawn, and they are semelparous (that is, they die after spawn-

ing once). More than 95% of the body mass of Pacific salmon is accumulated from the marine environment (Groot and Margolis 1991). This material is transported to and deposited in freshwater habitats where the salmon spawn and die, providing an important nutrient subsidy to freshwater and riparian ecosystems throughout the Pacific Northwest (Gresh and others 2000).

The biological significance of this nutrient subsidy has been long recognized for lakes rearing sockeye salmon (*O. nerka*) (Juday and others 1932; Stockner and MacIssac 1996). However, only recently has quantitative evidence been generated that suggests that marine-derived nutrients (MD-nutrients) positively affect the productivity of streams and riparian zones. In the last decade, the application of stable isotope analysis to this subject has enabled direct quantification of marine-derived nitrogen (MD-nitrogen) and carbon (MD-carbon) in streams and riparian zones (Kline and others 1990; Bilby and others 1996; Ben-David and others 1998). Regrettably, very few studies have examined the ecosystem consequences of the additional nutrients. However, these studies have demonstrated elevated biomass of aquatic invertebrates (Minakawa 1997; Minakawa and Gara 1999; Wipfli and others 1998), and production of fish (Bilby and others 1998) and riparian trees (Helfield and Naiman 2001) through the manipulation of carcass abundance or through comparisons of stream reaches with and without salmon.

The application of stable isotope analysis has been especially revealing (Kline and others 1990; Bilby and others 1996, 1998; Johnston and others 1997). Salmon are highly enriched with the heavier isotopic forms of nitrogen (N), carbon (C), and sulfur (S) (^{15}N, ^{13}C, ^{34}S, respectively) relative to contributions of these elements from other sources. As a result, the proportion of N, C, or S of marine origin in aquatic organisms, riparian vegetation, benthic organic matter, or dissolved in water can be determined. The stable isotope of S has been used less often than N or C due to a more tedious analytical procedure (MacAvoy and others 1998). Nevertheless, stable isotope analysis has firmly established that salmon often make a substantial contribution of nutrients to the streams and lakes where they spawn and rear, to the vegetation bordering the channel, and to various species of wildlife.

The scientific and policy significance of MD-nutrient subsidies by salmon to freshwater ecosystems is profound. The increased understanding of this complex system raises a number of important questions for both science and management. For example, what are the pathways for movement of MD-nutrients within the stream or lake, the adjacent riparian zone, and the downstream aquatic systems? How do MD-nutrients affect community composition, diversity, and productivity of invertebrate, resident fish, and plant communities? What are the roles and interactions with fish predators (that is, bears, otters, and birds) in the utilization and redistribution of MD-nutrients? Are the methods used to set salmon escapement goals and hunting guidelines adequate to ensure the long-term integrity of the entire salmon-producing system? These questions and concerns become especially pressing in light of the century-long decline in salmon populations throughout much of the Pacific Northwest (NRC 1996; Stouder and others 1996).

Our objectives for this review are threefold. First, after a brief overview of salmon population conditions, we summarize recent advances in understanding the linkages among MD-nutrients, freshwater and riparian ecosystems, and community dynamics. We begin by addressing the importance of MD-nutrients to lakes and streams. We then review large-scale and long-term processes in the atmosphere and ocean that govern variability in salmon population strength. Second, we evaluate the validity of the discoveries and examine their implications for active ecosystem management, noting areas where extrapolation of results still requires caution. Finally, we conclude by outlining key research areas where additional discoveries could greatly augment the understanding of processes that shape the structure and dynamics of salmon production and the characteristics of salmon habitats and associated riparian zones.

CURRENT STATUS OF SALMON POPULATIONS IN THE PACIFIC NORTHWEST

Decreases in the abundance of salmon over the last century have been well documented for California, Oregon, Idaho, and Washington (Nehlsen and others 1991; Nickelson and others 1992; NRC 1996). Some stocks in British Columbia and Alaska also have decreased, although most stocks north of the United States–Canada border are closer to their historic abundance than those to the south (Slaney and others 1996; Baker and others 1996). The average number of salmon returning to river systems south of British Columbia has decreased from approximately 45 million at the beginning of the 20th century to less than 2 million in recent years (Gresh and others 2000). Salmon have been eliminated from about 40% of their historic range in these states, and population levels are considered to be stable in only 16% of the area (NRC 1996).

Table 1. Historical and Current Estimated Range of Biomass, N, and P Delivered by Spawning Salmon to Watersheds in California, Oregon, Idaho, and Washington

	Historic	Current
Biomass (Mt)	156,000–254,298	11,843–13,747
N (Mt)	4853–6854	360–418
P (Mt)	574–810	43–49

N, nitrogen; P, phosphorus
Data from Gresh and others (2000)

Declines in salmon abundance have caused a corresponding decrease in the amount of nutrients and organic matter delivered by salmon to freshwater ecosystems. Gresh and others (2000) estimate that the deposition of nutrients by spawning salmon is now only about 7% of historical levels in watersheds in California, Oregon, Idaho, and Washington (Table 1). Even in areas that generally have not experienced dramatic declines in stock abundance, nutrient deficiencies due to decreased salmon populations may still occur in some watersheds. An extensive survey of nutrient delivery by spawning salmon to British Columbia streams has documented large decreases in watersheds where populations have not been enhanced by hatchery supplementation, fertilization, the construction of spawning channels, or other mitigating action (Larkin and Slaney 1997).

The history of salmon returning to the Willapa Bay watershed (southwest Washington) provides a representative example of this issue. The number of spawning chum (*O. keta*), coho (*O. kisutch*), and Chinook salmon (*O. tshawytscha*) using the tributaries declined from about 475,000 fish annually in the early 20th century to about 40,000 fish by the early 1990s (NRC 1996). Deposition of carcass biomass in these streams decreased from approximately 2650 Mt to 205 Mt, and contributions of MD-nitrogen and MD-phosphorus decreased by more than 90%. Similar scenarios could be described for many other watersheds.

MD-NUTRIENTS AND THE DYNAMICS OF SALMON-REARING LAKES

The importance of MD-nutrients to aquatic systems was first recognized in lakes where sockeye salmon rear for 1–2 y before migrating to the ocean. Over 70 years ago, Juday and others (1932) established the potential significance of nutrient deposition from salmon carcasses and estimated that spawning sockeye transported more than 2 million kg of organic matter and 5000 kg of phosphorus (P) annually to the Karluk Lake system in Alaska. Later, Donaldson (1965) pointed out that the P in sockeye carcasses represented a major component of the nutrient cycle of Lake Iliamna, the largest sockeye nursery lake in Alaska. Similarly, Krohkin (1975) provided early estimates of the major contributions of MD-phosphorus to the nutrient cycles of sockeye-bearing lakes throughout the Kamchatka Peninsula of northeastern Russia. Krohkin's work was especially focused on Lake Dalnee, where he estimated that spawning sockeye contributed 30%–40% of the annual P inputs to the system.

A small proportion of the nutrients contributed to nursery habitats from adult carcasses is exported by smolts migrating from lakes to the ocean. For example, we calculate that adult sockeye salmon carcasses from 1957 to 1998 in Lake Iliamna, Alaska contributed 7×10^7 kg of N and 3.3×10^6 kg of P. Migrations of smolts from Lake Iliamna during this same period represent losses of 1.1×10^6 kg of N and 2.2×10^5 kg of P. These rates translate into a nutrient imbalance that results in about 15 times more N and P being deposited in the freshwater ecosystem by adult salmon than is returned to the ocean via smolt migrations. The relative magnitude of difference in MD-nutrients between that contributed by spawning salmon and that exported by smolts is likely to be comparable in other systems with healthy sockeye populations. This imbalance would have been even more skewed before the 20th century, when industrial fisheries developed and intercepted much of the nutrients in salmon before they reached spawning grounds.

Feedbacks from MD-nutrients to Ecosystem Processes in Lakes

The lakes in which juvenile sockeye salmon rear are typically oligotrophic, and primary production is often severely nutrient-limited (Goldman 1960; Hyatt and Stockner 1985; Wurtsbaugh and others 1997; Gross and others 1998). Thus, nutrient inputs from salmon carcasses have the potential to substantially stimulate lake primary productivity. However, data demonstrating a clear link between spawning population size and lake productivity are sparse. Nevertheless, Schmidt and others (1998) showed a clear correlation between total-P concentration and salmon escapement in the previous year, which translates into increased phytoplankton biomass as well. Similarly, Krohkin (1975) showed that several continuous years of poor sockeye returns results in a 20% decrease in primary

production. Alaskan Peninsula lakes that, due to natural blockages, do not have sockeye salmon have total-P concentrations 33% lower than similar systems with sockeye runs (total phosphorus 4 μg/L ($n = 13$) versus 6 μg/L ($n = 57$) (Kyle 1996). This difference in nutrient level corresponds to about a doubling of phytoplankton standing stock (0.5 μg chl a/L versus 1.1 μg chl a/L) and suggests that a nutrient deficit from a lack of adult carcasses limits primary production in systems without anadromous salmon (Kyle 1996).

The responses of zooplankton to changes in adult densities (and MD-nutrient fluxes) are more inconsistent than the observed responses by phytoplankton. These inconsistencies probably result from confounding interactions between fertilization by salmon carcasses and predation from the numerous juvenile sockeye produced from large adult escapements. Management programs in Alaska that stock juvenile sockeye into "barren lakes" (that is, lakes with natural blockages to salmon migration) provide an opportunity to evaluate the effects of juvenile sockeye predation on zooplankton communities. Kyle (1996) confirms that relatively modest stocking rates of juvenile sockeye have substantial predation effects on zooplankton communities. In general, when juvenile salmon are introduced to lakes without the fertilizing effects of adult carcasses, zooplankton communities are shifted to smaller-bodied species and from cladocerans to copepods. Unfortunately, phytoplankton responses in the stocking experiments have not been documented. In Lake Dalnee, Kamchatka, decreases in annual primary production associated with periods of low sockeye salmon returns translate into a 30% decrease in annual production of zooplankton and a 45% decrease in total annual production of plankton-eating fishes, including juvenile sockeye (Krokhin 1975). In Karluk Lake, Alaska, the adult density of sockeye salmon has a strong negative effect on zooplankton biomass in the year following spawning in response to predation by higher densities of planktivorous fry (Schmidt and others 1998).

Responses of other components of lentic food webs to changes in MD-nutrient fluxes are virtually unexplored. Studies using ^{15}N to trace MD-nutrients in lentic food webs have demonstrated that MD-nitrogen is distributed throughout the resident fishes and benthos of systems with large sockeye spawning runs (Mathisen and others 1988; Kline and others 1993; D. E. Schindler unpublished). This ^{15}N enrichment of lentic food webs results from the direct consumption of dead salmon tissue by fishes and benthic insects, as well as the incorporation of MD-nitrogen into lentic food webs following the release of dissolved nutrients from decomposing carcasses and their subsequent uptake by primary producers. Although these comparative studies demonstrated the distribution of MD-nitrogen among ecosystem components, they did little to elucidate the effects of MD-nitrogen on the dynamics of lentic food webs. The mechanisms by which MD-nutrients in salmon carcasses move through benthic and pelagic food webs of lakes and the consequences of this process for ecosystem dynamics are critical areas for future research.

Deposition of MD-nutrients in nursery lakes may provide a positive feedback to juvenile salmon growth and survival and thus sockeye population dynamics. Growth and survival of juvenile sockeye in lakes are positively related to temperature, food resources, and primary productivity (Burgner 1987; Koenings and Burkett 1987; Kyle and others 1988; Hume and others 1996). Nevertheless, only one study has established a clear link between MD-nutrient deposition and long-term recruitment of sockeye salmon. Schmidt and others (1998) show convincing evidence that long-term reduction of the sockeye salmon population in Karluk Lake has substantially reduced P availability, resulting in depressed primary and secondary production. They suggest that this depression of primary and secondary production depresses the overall productivity of the sockeye population.

Analyses have suggested that maximum sustainable yield (that is, the largest sustainable harvest rate) of sockeye is highest when adult escapement exceeds approximately 800,000 individuals in Karluk Lake. This escapement level translates into a spawning density of more than 20,000 fish km^{-2} where carcasses contribute about 90% of the P load to Karluk Lake. Comparative studies of sockeye smolts from several lakes in Alaska demonstrate a clear positive association between spawning density and the concentration of MD-nitrogen in smolts (Finney and others 2000). However, aside from the Karluk Lake study, there is still no clear indication that increased MD-nutrient fluxes translate into a higher capacity for nursery lakes to produce sockeye salmon. Although this link between the deposition rate of MD-nutrients and fish production seems logical from the basics of ecological principles, it has yet to be clearly demonstrated.

Advances from Paleolimnology

Recent advances in paleolimnology have greatly enhanced our understanding of long-term variability in sockeye population dynamics and the loading of MD-nutrients to lakes (Finney and others 2000).

Upon carcass decomposition, the enriched δ^{15}N in salmon carcasses is incorporated into local food webs (Kline and others 1993) and eventually accumulates in lake sediments (Finney 1998). In most lakes, the organic component of sediments is dominated by the settling of plankton from the water column and in situ production by benthic algae—both of which readily use N released from salmon carcasses. Thus, lake sediments represent an integrated chronology of information about the inputs of MD-nitrogen and historical lake production.

Paleolimnological analyses of sedimentary δ^{15}N records as a means of reconstructing the long-term population dynamics of sockeye salmon in several Alaskan lakes have shown a substantial reduction in the quantity of MD-nutrients since the rise of commercial fishing at the beginning of the 20th century (Finney and others 2000). Associated with the reduction in MD-nutrients are apparent changes in zooplankton and algal communities. For example, a shift toward dominance by benthic diatoms suggests a reduction in pelagic primary production related to the expansion of commercial fishing. Fossil densities of cladoceran zooplankton suggest a fertilizing effect of MD-nutrients on *Bosmina longirostris* (Finney and others 2000); however, this result should be viewed with some reservation because much of the zooplankton community in Karluk Lake is composed of copepods that do not form fossils in the sedimentary records.

The δ^{15}N signature in salmon carcasses and the subsequent storage of MD-nitrogen in lake sediments provide several powerful applications that can be used to study ecosystem processes over broad temporal and spatial scales. For example, temporal variability in salmon population dynamics associated with the effects of low-frequency climate variability on marine productivity (for example, the Pacific Decadal Oscillation [PDO]) (Mantua and others 1997) can be reconstructed from δ^{15}N records in lake sediments (Finney and others 2000). In systems where the spawning densities of sockeye are known from historical spawning ground surveys, the rates of N loading from watersheds can be estimated by treating MD-nitrogen as a natural tracer. Historical salmon escapements are not related linearly to δ^{15}N records in lake sediments, as is often assumed. Instead, multiple-source mixing models must be used to translate sediment isotope records into reconstructions of historical salmon densities. Below, we briefly describe how this is accomplished.

A two-source mixing model (Lajtha and Michener 1994) is used to estimate the response of the δ^{15}N signature of lake sediments to changes in the density of spawning salmon. This mass-balance model assumes that lake sediments accumulate N from marine sources (that is, via salmon carcasses) and from a combined pool of other sources that includes the watershed and the atmosphere. The model also assumes that there is no internal feedback from the deposition of MD-nitrogen to other N-related processes in lakes (for example, it assumes that MD-nitrogen does not stimulate denitrification). The relative contributions of marine-derived and background N to the sediment pool are assumed to be proportional to the relative input rates from each of these pools. The isotopic signature of the sediments ($^{15}N_{sed}$) can be calculated as:

$$^{15}N_{sed} = (^{15}N_{mdn} - {}^{15}N_b) \cdot (X_{mdn}/(X_{mdn} + X_b)) + {}^{15}N_b$$

$$(1)$$

where $^{15}N_{mdn}$ is the isotopic signature of MD-nitrogen in salmon carcasses (δ^{15}N in ‰), $^{15}N_b$ is the isotopic signature of all N sources other than salmon (δ^{15}N in ‰), X_{mdn} is the loading rate of N from spawning salmon (kg N km^{-2} y^{-1}), and X_b is the background loading rate of N from other sources to the lake (kg N km^{-2} y^{-1}). The background loading rate of N can then be estimated by measuring $^{15}N_{mdn}$ from salmon carcasses, $^{15}N_b$ from the sediments of reference lakes without salmon, and X_{mdn} from historical spawning counts. Applying this model to data presented by Finney and others (2000) allows us to compare sediment δ^{15}N to spawning densities (Figure 1). In estimating the background N-loading rate, it is assumed that $^{15}N_{mdn} = 12$‰, the value for sockeye salmon, and $^{15}N_b = 1.5$‰, based on the δ^{15}N signature of surface sediments from Alaskan lakes that do not have anadromous salmon runs (Finney and others 2000). N loading from salmon carcasses (X_{mdn}) is calculated as the product of spawning density (number · km^{-2}y^{-1}) and the N content of an average sockeye salmon (0.07 kg N · adult^{-1}). The background N-loading rate (X_b) is then estimated by maximum likelihood. This model produces an asymptotic response of δ^{15}N in lake sediments to increases in spawning density (Figure 1A). Based on this model, it is estimated that these sockeye-bearing lakes in Alaska receive an average of 1521 kg N · km^{-2} · y^{-1} from sources other than salmon carcasses. This N-loading rate can be used as the background to which MD-nitrogen loading can be compared. Based on the 12 lakes presented by Finney and others (2000), it is estimated that N loading from sockeye carcasses currently contributes about 25% of the N in sockeye nursery lakes,
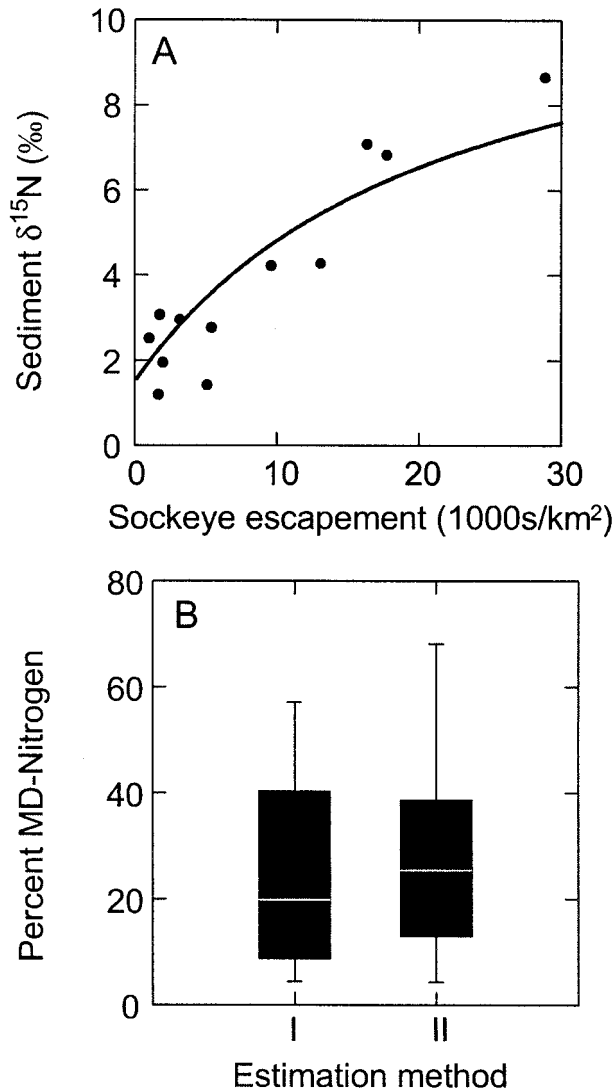
Figure 1. (A) Relationship between spawning density of sockeye salmon and the stable N isotope characteristics of surface sediments in 12 Alaskan lakes. Data were digitized from Finney and others (2000). The curve is the best fit of a two-box mixing model to these data (see text, Eq. (1); $^{15}N_{sed} = 10.5 \cdot (esc/(esc+ 21.7)) + 1.5$. $r^2 = 0.78$, where esc is the spawning density of salmon in thousands of fish per km^2. The value 1.5 is the average $\delta^{15}N$ of surface sediments from lakes without salmon, and salmon were assumed to have a $\delta^{15}N$ of 12‰). (B) Box plots of the percent of all N inputs that are provided by sockeye salmon carcasses for the lakes presented in A based on two calculation methods. Method I compares the N inputs from sockeye to the overall estimate of background N-loading for all lakes simultaneously (that is, from the curve presented in A). Method II estimates the percent contribution of N from sockeye by applying the two-source mixing model individually to each lake. The mean, median, and standard deviation for Method I are 25.0, 19.9, and 18.4, respectively, and 27.7, 25.4, and 20.7, respectively, for Method II.

but the figure can be as high as 70% in lakes with high spawning densities (Figure 1B).

Overall, expectations about links between sockeye salmon carcass deposition and lake productivity are relatively direct—based on the fact that nursery lakes are usually nutrient-limited (Goldman 1960) and salmon carcasses can be a major component of nutrient budgets. The responses of different lakes to carcass nutrients will depend on their hydrology and the relative loading of N and P from their watersheds. Most sockeye nursery lakes are P-limited, but the constraints of P limitation relative to N limitation will depend on the development of vegetation in watersheds (especially if N-fixers such as alder, *Alnus* spp., are present), P loading from other sources such as volcanoes, and landscape position. It follows that carcass deposition also should enhance the rearing capacity of nursery lakes for juvenile sockeye (Stockner and MacIsaac 1996). However, the links between MD-nutrients and sockeye population dynamics remain uncertain. Feedback between MD-nutrients and sockeye population dynamics may account for the long-term declines in populations seen in some systems (for example, see Schmidt and others 1998), but their generality needs to be explored in other systems.

THE ROLE OF MD-NUTRIENTS IN STREAMS

In contrast to lakes, the influence of spawning salmon on the nutrient dynamics and biological productivity of streams and rivers was not a widespread research topic until 1990, although the potential significance of this nutrient subsidy in oligotrophic streams had been demonstrated earlier (Richey and others 1975). The application of stable isotope methods has established that salmon can make large contributions of nutrients and organic matter to streams (Kline and others 1990; Bilby and others 1996), riparian vegetation (Ben-David and others 1998; Helfield and Naiman 2001; Bartz 2002), and wildlife (Ben-David and others 1997; Hilderbrand and others 1996). More recent research has begun to determine the ecological responses to these nutrient subsidies.

Contribution of MD-nitrogen by Spawning Salmon

The proportion of MD-nitrogen in various stream components is directly related to the density of fish spawning at that site and inversely related to the time since spawning fish were present. In tributaries to the Stuart River in British Columbia, the
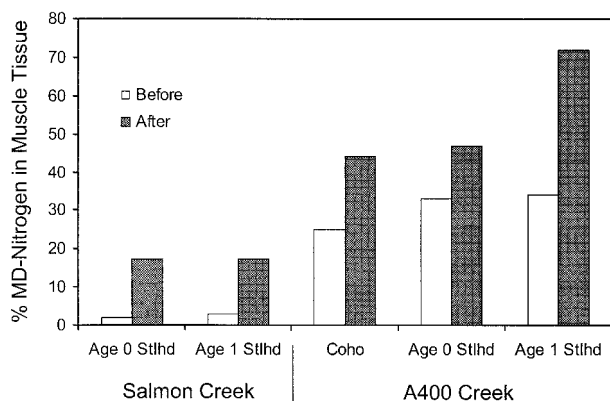
Figure 2. Increase in the proportion of salmon-derived N in the dorsal muscle of juvenile steelhead and salmon in two streams in southwestern Washington to which salmon carcasses were added. Before values indicate the proportion prior to addition of carcasses; the after value represents the proportion after carcasses had fully decomposed (about 6 weeks after carcass addition). The proportion of MD-nitrogen was estimated from N stable isotope ratios. The higher pre-addition values at A400 Creek are likely due to the higher abundance of naturally spawning salmon at this site than at Salmon Creek. Data from Bilby and others (1998).

proportion of MD-nitrogen in insects and juvenile fishes was found to increase with increasing numbers of spawning sockeye salmon (Johnston and others 1997). This relationship is not linear; the proportion of MD-nitrogen increases rapidly with carcass deposition at low spawning densities and increases at a much slower rate at very high densities. This relationship also has been demonstrated for juvenile coho salmon in streams in Washington (Bilby and others 2001).

Seasonal changes in the proportion of MD-nitrogen in stream biota can be substantial. Rainbow trout (*O. mykiss*) in a southeast Alaska stream were found to contain about 75% MD-nitrogen, and periphyton and caddisflies contained from 30% to 50% MD-nitrogen prior to the arrival of large numbers of pink salmon (*O. gorbuscha*; Kline and others 1990). Following salmon spawning, nearly all of the N in the trout, periphyton, and insects at this site is from the spawning fish. Similarly, the proportion of MD-nitrogen in the muscle tissue of juvenile coho salmon and steelhead increased dramatically and rapidly following the addition of salmon carcasses to two streams in southwestern Washington (Bilby and others 1998) (Figure 2).

MD-nitrogen persists in streams throughout the year. The early autumn $\delta^{15}N$ of cutthroat trout (*O. clarki*) in streams where coho salmon spawn in late

autumn is enriched with ^{15}N relative to cutthroat trout in stream reaches inaccessible to salmon in the same watershed, indicating the presence of MD-nitrogen (Bilby and others 1996). The juvenile coho salmon in this watershed exhibit a $\delta^{15}N$ signature that indicates that approximately 33% of the N in the food they consume after emergence from the gravel in March is of marine origin. No carcasses are present in the stream over this period.

Some of the mechanisms that contribute to the retention of MD-nutrients in streams have been identified. MD-nitrogen has been found in the fruit and foliage of riparian plants in Washington (Bilby and others 1996) and coastal Alaska (Ben-David and others 1998; Helfield and Naiman 2001; Bartz 2002). The proportion of MD-nitrogen in riparian plants varies with distance from the channel and among species, but it may constitute up to approximately one-third of the total N in the plants (Table 2). MD-nutrients stored in the terrestrial environment can be delivered to the stream in litterfall, throughfall, or groundwater. Long-term storage within the aquatic environment also may occur. Dissolved organic matter released by decomposing salmon carcasses is rapidly sorbed onto the epilithic organic matter layer that encrusts the streambed (Bilby and others 1996). This organic layer also occurs on hyporheic surfaces, providing a potentially huge area for the collection and retention of MD-nutrients (Edwards 1998). Mineralization of the hyporheic organic matter film or fragmentation into fine particles by invertebrates would enable transport of these materials to surface waters. The extent to which various processes contribute to the retention of MD-nutrients in streams is not known. However, the stable isotope evidence demonstrating the presence of MD-nutrients in streams throughout the year indicates that long-term storage is occurring.

Uptake Processes

The materials transported to streams by spawning salmon are incorporated into the trophic system via two pathways: (a) direct consumption of carcass flesh and salmon eggs by fish and invertebrates, and (b) chemical or biological uptake of dissolved materials released by fish metabolism and by carcass decomposition.

Juvenile salmon and trout and invertebrates will ingest eggs or flesh from spawning salmon (Figure 2). When salmon eggs or carcass flesh are available, these materials often comprise the majority of the diet of stream-dwelling salmonids (Eastman 1996). For example, in a southwest Washington stream, over 60% of the stomach contents of juvenile coho

Table 2. Range of Reported Average Values for % MD-nitrogen in Riparian Foliage along Salmon Spawning Streams

Species	% MD-Nitrogen	Reference and Location
Salmonberry (*Rubus spectabilis*)	18	Bilby and others 1996[a] (Washington)
Devil's club (*Oplopanax horridum*)	18–22	Bilby and others 1996[a] (Washington); Helfield and Naiman 2001 (SE Alaska)
White spruce (*Picea glauca*)	16–24	Hilderbrand and others 1999 (Alaska); Helfield 2001 and Bartz 2002 (SW Alaska)
Sitka spruce (*P. sitchensis*)	24	Helfield and Naiman 2001 (SE Alaska)
Western hemlock (*Tsuga heterophylla*)	18–20	Bilby and others 1996[a] (Washington); Helfield 2001 (SW Alaska)
Balsam poplar (*Populus balsamifera*)	24	Helfield 2001 (SW Alaska)
Red alder (*Alnus rubra*)	1	Helfield and Naiman 2001 (SE Alaska)
Green alder (*A. crispa*)	<1	Helfield 2001 (SW Alaska)
Fern (*Dryopteris dilatata, Athyrium felix-femina*)	22	Helfield and Naiman 2001 (SE Alaska)
Feltleaf willow (*Salix alaxensis*)	17–26	Helfield 2001 and Bartz 2002 (SW Alaska)
Littletree willow (*Salix arbusculoides*)	14	Bartz 2002 (SW Alaska)
Highbush cranberry (*Viburnum edule*)	13	Bartz 2002 (SW Alaska)
Cow parsnip (*Heracleum lanatum*)	17	Bartz 2002 (SW Alaska)
Polar grass (*Arctagrostis latifolia*)	24	Bartz 2002 (SW Alaska)

Single values signify only one study.
[a]*Values from a composite sample of salmonberry, devil's club, and western hemlock foliage*

salmon and over 90% of the stomach contents of juvenile steelhead consisted of salmon eggs and carcass flesh while coho salmon carcasses were present (Bilby and others 1998).

Carcass flesh and eggs are consumed by a wide variety of aquatic invertebrates. Chironomids have been found to feed on both eggs (Elliott and Bartoo 1981) and carcass flesh (Piorkowski 1995). Large stoneflies (family Pteronarcidae) ingest carcass flesh (Minakawa 1997), and several species of the normally predaceous stonefly *Alloperla* scavenge dead salmon eggs and alevins but rarely ingest live eggs or alevins (Nicola 1968). Several species of limnephilid caddisfly larvae are often found on salmon carcasses, sometimes at very high densities (Brusven and Scoggin 1969; Piorkowski 1995; Minakawa 1997). These insects first invade the gill cavity and mouth, and as the carcass decomposes, they are found on all external surfaces. The caddisflies ingest both the microbes covering the surface of the carcass and the flesh (Piorkowski 1995; Minakawa 1997).

Spawning salmon contribute large quantities of dissolved matter to streams during spawning and during decomposition of the carcasses (Mathisen and others 1988). There are a variety of processes by which the dissolved material released by fish metabolism and decomposing salmon carcasses can be captured and incorporated into the trophic system. Uptake of inorganic nutrients by stream autotrophs (algae and vascular aquatic plants) is an important mechanism in some systems (Richey and others 1975; Schuldt and Hershey 1995; Johnston and others 1997). Dissolved organic matter released by decomposing salmon carcasses also is assimilated by heterotrophic organisms growing on the carcass (Piorkowski 1995) as well as on the streambed (Schuldt and Hershey 1995); chemical sorption onto the organic matter film encrusting streambed and hyporheic surfaces also occurs (Bilby and others 1996).

The predominant uptake mechanism for dissolved matter generated by salmon varies with the time of year that spawning occurs. Chemical sorption of dissolved organic matter onto the streambed substrate was found to be the most important uptake mechanism for material released by coho salmon carcasses during November and December in a western Washington stream (Bilby and others 1996). Low water temperatures and light levels and high stream discharge reduce the effectiveness of biological uptake processes at this time of year. Biological processes dominate during warmer, brighter months. Autotrophic and heterotrophic processes are primarily responsible for the uptake of dissolved organic matter released by decomposing Chinook salmon carcasses in early autumn (Schuldt

Table 3. Proportion of N and P in the Foliage of Herbaceous Plants along Streams with and without Salmon

Location and Nutrient	With Salmon (% dry weight $\pm$ SE)	Without Salmon (% dry weight $\pm$ SE)
Griffin Creek[a]		
N (salmonberry)	2.6 $\pm$ 0.3	2.2 $\pm$ 0.4
P (salmonberry)	0.20 $\pm$ 0.05	0.15 $\pm$ 0.03
Kennedy Creek[a]		
N (salmonberry)	2.3 $\pm$ 0.2	2.0 $\pm$ 0.2
P (salmonberry)	0.22 $\pm$ 0.08	0.14 $\pm$ 0.02
Tenakee Inlet[b]		
N (devil's club)	2.8 $\pm$ 0.10	2.5 $\pm$ 0.06
N (ferns)[c]	2.6 $\pm$ 0.18	2.1 $\pm$ 0.10

N, nitrogen; P, phosphorus

Values from western Washington watersheds (Griffin and Kennedy creeks) represent averages of approximately 50 samples for each site and treatment collected from the channel edge and at 20 m, 50 m, and 100 m from the channel. Values for N from the southeastern Alaska sites (Tenakee Inlet) represent averages of approximately 10 samples taken within 25 m of the streams. Concentrations of N and P at all streams are significantly higher at sites with salmon than at sites without salmon (t-test; P < 0.05). However, these are basically N-limited systems. In the dominantly P-limited systems of southwestern Alaska (data not shown), there are few significant differences between streams with and without salmon in the proportion of N and P in common riparian plants (Bartz 2002).

[a]*R. F. Bilby (unpublished)*
[b]*Helfield and Naiman (2001)*
[c]*Fern species are* Dryopteris dilatata *and* Athyrium felixfemina.

and Hershey 1995) and sockeye salmon carcasses in midsummer (Johnston and others 1997).

Ecological Influence of MD-nutrients

Elevated primary production due to nutrients from salmon metabolism and carcasses has been noted in a number of oligotrophic systems. Kokanee salmon (landlocked *O. nerka*) carcasses stimulated algal production in a small tributary of Lake Tahoe, California-Nevada (Richey and others 1975), and the addition of 25 Chinook salmon carcasses to a tributary of Lake Superior, Minnesota, resulted in increased chlorophyll *a* in the epilithic organic matter layer (Schuldt and Hershey 1995). Carcasses have little effect on primary production in nutrient-rich streams (Rand and others 1992). The increase in primary production and the availability of carcasses and eggs as a food resource also influence aquatic invertebrates. Invertebrate density and biomass from late spring through early autumn are greater in streams where coho salmon spawn than in similar streams inaccessible to salmon (Minakawa 1997).

The increase in invertebrate production and the direct food subsidy represented by the carcass flesh and eggs of spawning salmon increases food availability for stream fishes. Adding carcasses of hatchery coho salmon to a small stream in southwestern Washington doubled the growth rate of juvenile coho relative to a nearby stream reach with a low availability of carcasses (Bilby and others 1998).

Fish residing at the carcass-addition site contained nearly 20 times the amount of material in their stomachs than did fish collected from the site with few carcasses; 60%–95% of this material consisted of salmon eggs and flesh. Rapid increases in the proportion of MD-nitrogen in the juvenile fish at the treated site (Figure 2) and the abundance of eggs and flesh in their stomachs clearly indicate that the material derived from the carcasses is responsible for the accelerated growth rate.

Increasing the body size of juvenile salmonids can significantly increase their survival. Larger body size is positively correlated with the over-winter survival of juvenile coho salmon (Hartman and Scrivener 1990; Quinn and Peterson 1996), and larger smolts survive to maturity at a much higher rate than smaller smolts (Bilton and others 1982; Ward and Slaney 1988; Holtby and others 1990; Tipping 1997). Thus, the influence of MD-nutrients on the growth of juvenile salmon may generate a positive feedback loop as increased survival generates progressively higher levels of deposition of MD-nutrients (Bilby and others 1996).

Transport of MD-nutrients into Riparian Ecosystems

Salmon also make a measurable contribution to the nutrient capital of riparian ecosystems. The N concentration of devil's club (*Oplopanax horridus*) and ferns (*Dryopteris dilatata and Athyrium felix-femina*) in Alaska is higher along salmon-bearing reaches than
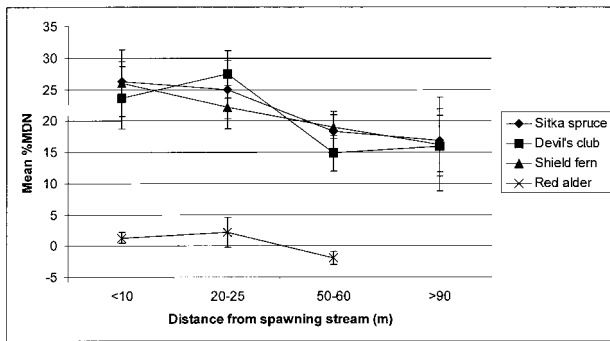
Figure 3. Percent MD-nitrogen ($\bar{x} \pm SE$) as a function of lateral distance from spawning streams for Sitka spruce (*Picea sitchensis*), devil's club (*Oplopanax horridus*), shield fern (*Dryopteris dilatata*), and red alder (*Alnus rubra*) at Tenakee Inlet, Alaska. Data from Helfield and Naiman (2001).

in stream sections inaccessible to salmon (Table 3). Stable isotope data indicate that at least some of this difference can be attributed to nutrients contributed by salmon (Bilby and others 1996; Ben-David and others 1998; Helfield and Naiman 2001). MD-nitrogen can be distributed at a considerable distance from the channel. The extent of upslope distribution of MD-nitrogen on Chichagof Island, Alaska, varies by site and plant species and is influenced by the presence of piscivorous predators (Ben-David and others 1998). At this and other locations in coastal Alaska, MD-nitrogen is found in some plant species up to 200 m from the channel edge (Helfield and Naiman 2001; Bartz 2002) (Figure 3).

Alterations in the production and diversity of plant communities along stream reaches with salmon have been attributed to nutrient contributions made by the fish. Helfield and Naiman (2001) found that the growth rates of Sitka spruce (*Picea sitchensis*) were three times faster adjacent to an Alaskan river with spawning salmon than along nearby sites without salmon (Table 4). At the salmon-spawning sites, it takes only 86 years for Sitka spruce to reach a diameter of 50 cm (that is, a size where woody debris contributes substantially to the creation and maintenance of salmonid habitat in the river), as opposed to 307 years at sites without salmon. Cover and diversity of understory vegetation and shrubs in riparian areas also may be influenced by the nutrient subsidy provided by salmon (Bartz 2002). Overstory basal area and stem density are greater below barriers where salmon spawn, whereas shrub basal area and stem density, as well as understory species richness and evenness, are greater above spawning barriers.

There are numerous interacting mechanisms that

contribute to the distribution of MD-nutrients in riparian systems (Ben-David and others 1998; Helfield and Naiman 2001). Floods may deposit carcasses in the riparian areas, especially at sites where spawning occurs at times when periods of high discharge are common (Cederholm and others 1989). Nutrients released from spawning fish and from carcasses decomposing in the stream may be carried into the hyporheic zone beneath the riparian area. MD-nutrients become available to the riparian vegetation where the roots of the plants extend into the hyporheic zone. However, the few data collected to date suggest that this may not be a primary pathway except during peak spawning runs. Ongoing research suggests that the actual importance of this pathway will depend on local physical conditions and the number of spawning fish (T. O'Keefe and R. Edwards unpublished). In contrast, various animals capture a large number of spawning fish or scavenge carcasses and carry them into the riparian area, where they are consumed or cached for later use (Ben-David and others 1998). Cederholm and others (1989) found that 40% of the coho salmon carcasses in several small Olympic Peninsula streams were removed from the water by scavengers; most were deposited in the riparian area. Stable isotope analysis of N in hair and bone samples from grizzly bear (*Ursus arctos horribilis*) killed in the Columbia River basin between 1856 and 1931 indicated that 33%–90% of the N in the diet of these animals was from salmon (Figure 4). Comparatively, more than 90% of the N in the diet of coastal brown bears (*Ursus arctos*) in Alaska is from salmon (Hilderbrand and others 1996). These values may not represent the proportion of diet composed of salmon because some of the MD-nitrogen is likely obtained from riparian plants that have incorporated MD-nutrients. MD-nutrients are made available to the vegetation as the unconsumed portion of the carcass decomposes or by deposition of waste products (primarily urine) from the animals that ate the carcass (Hilderbrand and others 1999). In addition to these mechanisms of transport, MD-nutrients incorporated by riparian plants also can be moved progressively upslope by litterfall or by direct root transfer.

## LARGE-SCALE PROCESSES AND THE ABUNDANCE OF PACIFIC SALMON

Variations in salmon abundance and MD-nutrient subsidies to freshwater systems are strongly influenced by complex processes coupling atmospheric patterns with marine and freshwater ecosystems. Only recently, however, have the important influ-

Table 4. Growth Rates of Sitka Spruce within 25 m of Streams with and without Spawning Salmon

Growth Parameter	Sites with Salmon	Sites without Salmon
Basal area growth ($cm^2/y \pm 1$ SE)	22.93 ± 3.07	6.39 ± 1.82
dbh (cm $\pm$ 1 SE) at 100 years	54 ± 3.5	29 ± 3.8
Years ($\pm$ 1 SE) to attain 50 cm dbh	86 ± 10.1	307 ± 68.1

dbh, diameter at breast height
Data summarized from Helfield and Naiman 2001
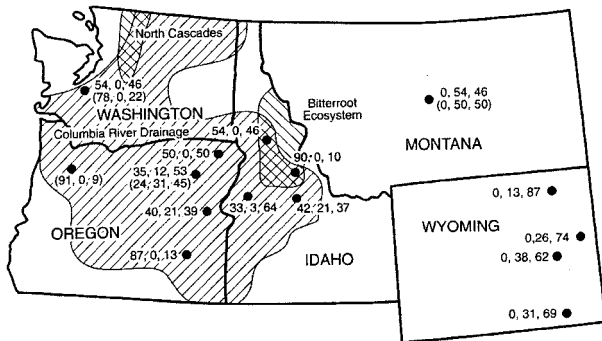
Figure 4. Historical composition of the diet of grizzly bears throughout the northwestern United States for animals killed between 1856 and 1931. Diet percentages are estimated from the stable isotope characteristics of bone collagen or hair samples (shown in parentheses). Each set of numbers refers to the percent contribution from salmon, terrestrially produced meat, and vegetation for bears at each location. The shaded area of the map refers to historical salmon spawning regions. From Hilderbrand and others (1996), with permission of the *Canadian Journal of Zoology.*

ences of shifts in atmospheric and oceanic conditions on salmonid populations been appreciated. Relatively short-term variability in climate conditions associated with season and with El Niño–Southern Oscillation (ENSO) events is apparent in the dynamics of salmon and their ecosystems (Mysak 1986; Drake and others, forthcoming). There is strong evidence that decadal and longer modes of cyclical variability in the characteristics of marine ecosystems greatly influence the growth and survival of Pacific salmon during a major portion of their life cycle (Mantua and others 1997; Francis and others 1998; Beamish and others 1999). These variations have important implications for freshwater systems.

The Northeast Pacific Ocean is particularly responsive to subdecadal (for example, ENSO) and interdecadal modes of variability (Mysak 1986; Mantua and others 1997; Minobe 1997, 1999). Pro-

longed modifications in ecosystem organization associated with interdecadal changes in atmospheric–oceanic coupling are referred to as "regimes". Minobe (1997, 1999) contends that for the last 3 centuries interdecadal variations in climatic conditions in the North Pacific have been driven by two interacting climate oscillations that result in abrupt regime shifts during simultaneous phase reversals of the two signals. Further, Minobe (1999) suggests that the two dominant oscillations have characteristic bidecadal (around 20-year) and pentadecadal (50–70-year) frequencies; these two frequencies interact to produce climatic regimes lasting 20–30 years. According to this hypothesis, the dominant periodicity of regime shifts is driven by the characteristic frequency of the pentadecadal oscillation, but the abruptness of regime shifts is punctuated by interactions with the bidecadal mode of variability.

During the 20th century, there have been four apparent interdecadal regimes in the Northeast Pacific coupled atmosphere–ocean system: 1900–24, 1925–46, 1947–76, and 1977–99 (Mantua and others 1997; Francis and others 1998; N. J. Mantua personal communication). The signature of these regimes is detectable in a number of atmospheric, oceanic, and biological variables (for example, see Peterson and others 1999); the most noteworthy is the PDO (Mantua and others 1997). When positive, the PDO is characterized by a deep winter Aleutian Low and a bipolar sea surface temperature (SST) anomaly pattern, with warm SST anomalies along the Pacific coast of the Americas and cold SST anomalies in the central North and South Pacific. These anomalies are of the opposite sign during the PDO's negative polarity.

Climatic variation associated with PDO regime shifts has substantial impacts on the physical structure and biological productivity of the North Pacific Ocean. For example, the 1976–77 regime shift reduced Northeast Pacific atmospheric pressure at sea level by about 2 millibars and increased spring SST by about 0.2–0.4°C (Francis and others 1998). Small changes in SST, wind shear, and sea level

pressure during this regime shift translated into relatively large changes in the physical structure of the Northeast Pacific Ocean (Polovina and others 1995). This regime shift corresponded with a 20%–30% shoaling of the mixed layer in the Alaskan Current domain of the Northeast Pacific. This latter pattern resulted in a relaxation of light limitation on phytoplankton production (Polovina and others 1995) and a near doubling of zooplankton biomass in the Gulf of Alaska (Brodeur and Ware 1992; Roemmich and McGowan 1995; Brodeur and others 1996; Sugimoto and Tadokoro 1997).

There are strong and coordinated responses of salmonid production to the changes in atmospheric-oceanic coupling that are associated with regime shifts in the North Pacific (reviewed by Francis and others 1998; Beamish and others 1999). The best evidence for strong effects of regime shifts on production comes from detailed analysis of the 1976–77 event, when salmon production (as biomass and numbers) in the Northeast Pacific almost doubled (Beamish and Bouillon 1993; Hare and others 1999). Similarly, Gulf of Alaska groundfish biomass increased substantially during the early 1980s, leading to a more than 250% increase in commercial fishery catch in the 1990s (Anderson and Piatt 1999). Although the exact mechanisms responsible for population changes in salmon are not fully understood, the best evidence suggests that population dynamics are largely determined in the juvenile stages, when fish are most affected by climate-related changes in oceanic zooplankton production (Hare and others 1999).

Although total salmon production at the scale of the entire North Pacific basin appears to be linked synchronously to interdecadal regime shifts (Beamish and others 1999), there is evidence that salmon production in the northern (that is, Alaska Current) and southern (that is, California Current) regions oscillate out of phase with each other at interdecadal frequencies (Mantua and others 1997; Hare and others 1999) (Figure 5). This geographic organization of temporal variability has important long-term implications for salmon fisheries and for MD-nutrient subsidies to freshwater systems at the scale of the entire North Pacific basin. Future analyses of the geographic distribution and temporal changes in MD-nutrient subsidies must embrace these sources of long-term and broad-scale changes in the coupled atmosphere–ocean system that strongly regulates salmon populations throughout North America.

Large-scale climatic effects on salmon populations and their spatial distributions will also be mediated through freshwater ecosystem responses to
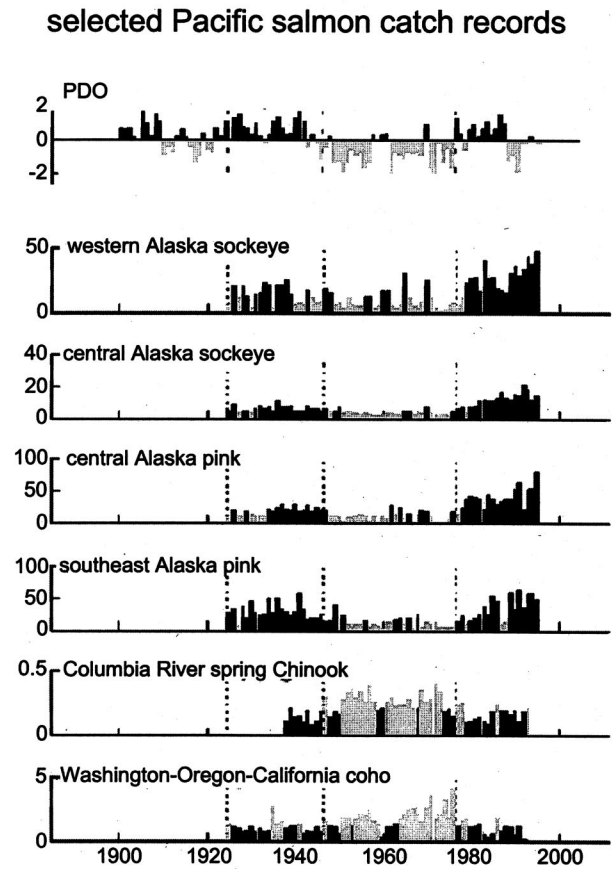

Figure 5. Synchronization of Pacific salmon catch records with the Pacific Interdecadal Oscillation (PDO) (from Mantua and others 1997, with permission) during the 20th century. Years with catches higher than the long-term median are shown by black bars for Alaskan waters; gray bars indicate Washington/Oregon/California fisheries. Vertical dotted lines mark the PDO reversal times (1925, 1947, and 1977). Total annual catches are expressed as millions of fish per year.

climate variation. Changes in precipitation patterns can be expected to have direct effects on the discharge regimes of freshwater ecosystems and thus the accessibility of spawning grounds to migrating salmon. Increases in stream and lake temperatures in response to climate warming,—or in the case of streams, forest harvest—will likely cause substantial changes in the growth and survival conditions for salmon. Systems located near the southern edges of the geographic distributions of salmon may warm to critical levels. The growth and survival of populations in northern ranges may actually increase in response to climate warming. As of yet, the responses of freshwater ecosystems to climate changes that control salmon population dynamics and spatial distributions are not as well understood

as those for the ocean. Recent syntheses (for example, see Melack and others 1997) offer some insight into these responses, but they are only superficially understood. Nevertheless, we expect that large-scale climatic regimes will have direct and important effects on salmon populations in both marine and freshwater environments. Salmon population responses to changing climate will directly alter the magnitude and ecological significance of the MD-nutrient subsidies we describe here.

CAUTIONS ON CURRENT UNDERSTANDINGS

There has been a recent divergence in research emphases concerning the role of MD-nutrients in freshwater ecosystems. Early research (prior to 1980) stressed the importance of salmon as sources of P to inland ecosystems because it was thought that most freshwater habitats used by salmon were P-limited. Recent studies have concentrated more on the transport of N, largely as a result of the development of stable isotope methods. Nitrogen has a useable stable isotope whereas P does not. The utility of MD-nitrogen as an ecological tracer cannot be overemphasized. However, future research must further embrace the complementary roles of N, P, and possibly other elements of biological significance. Salmon are relatively rich in P compared to N (the N:P ratio is approximately 5 by mass) and therefore are more likely to have bigger impacts on relative P availability than N availability. However, integrating tracer capabilities of elements having stable isotope pairs with investigations of the ecological importance of marine subsidies of elements without a stable isotope, such as P, will require more conceptual integration than has yet been accomplished.

Much of the evidence for the effects of MD-nutrients on freshwater and riparian ecosystems is represented by statistical correlation (across either space or time). This is especially true with respect to the spatial distribution of ^{15}N isotopes in ecosystems with varying densities of salmon. Although these data provide estimates to show where MD-nutrients accumulate in freshwater ecosystems, they tell little about the effects of MD-nutrients on ecosystem dynamics. Based on experience from other ecosystems, we expect that ecological responses to various levels of MD-nutrient input will probably involve many nonlinear or threshold responses, and that some species will be far more sensitive than others to changes in these subsidies. Deliberate, experimental manipulations of entire ecosystems (Carpenter and others 1995; Schindler and others 2000) provide the appropriate context for

understanding ecosystem responses to future changes in salmon populations.

There are three key areas where caution is warranted in the interpretation of the available data. These relate to isotopic fractionation of the N isotopes, the spatial and seasonal patterns of N versus P limitation, and lag times and legacies in salmon-influenced systems.

Fractionation of N-isotopes

In addition to MD-nitrogen inputs, soil δ^{15}N values are influenced by isotopic fractionation associated with microbial N processing which, in turn, is reflected in the stable isotope ratios of plants (Schulze and others 1994; Handley and Scrimgeour 1997). Microbial processes affecting soil δ^{15}N values vary spatially according to differences in slope, elevation, soil texture, and moisture. Microbes tend to process ^{14}N preferentially over ^{15}N, resulting in substrates that are ^{15}N-enriched relative to input N (Nadelhoffer and Fry 1994). Denitrification, in particular, entails relatively high rates of fractionation, resulting in ^{15}N-enriched nitrate pools (Mariotti and others 1981). This high fractionation rate is offset by relatively low fluxes (that is, low rates of denitrification) in most temperate forests, but ^{15}N enrichment may be significant at localized sites subject to periodic moisture saturation, such as floodplains. Fractionation may be negligible if N availability is the limiting factor for microbial processes, as all available N will be processed, regardless of isotopic composition. Similarly, uptake of ammonium or nitrate by plant roots will generally discriminate against the ^{15}N isotope, but this discrimination will be negligible where N limits plant growth (Nadelhoffer and Fry 1994).

These various processes affect the isotopic signature of plant tissues. For example, studies of non–salmon-bearing watersheds report increases in foliar δ^{15}N in plants growing in valley bottoms relative to more upland sites (Garten 1993). Foliar δ^{15}N of individual plants might also vary temporally as a result of N translocation and seasonal changes in the relative importance of storage and uptake. Intraseasonal variation in δ^{15}N is negligible for most species in most systems, but plants from high-N environments (for example, those in which salmon carcasses are abundant) may undergo significant changes in δ^{15}N over the growing season (Kielland and others 1998), potentially confounding assessments of MD-nitrogen contributions.

N- versus P-Limitation

Nitrogen is generally the nutrient that limits forest productivity in the Pacific Coastal Ecoregion (Weet-

man and others 1992). However, analysis of elemental ratios of N and P in stream systems in Washington indicates that either P or N availability may control primary production, varying by geologic substrate (Thut and Haydu 1971) and occasionally by season (Fevold 1998). In cases where N is not the limiting nutrient, the confounding effects caused by fractionation can compromise the ability to detect MD-nutrients in aquatic and riparian ecosystems using N stable isotope techniques. This problem may become especially significant in aquatic or riparian systems with high densities of N-fixing plants. In the Pacific Coastal Ecoregion, several species of alder are common along streams. Red alder (*Alnus rubra*), in particular, is found at high densities along stream systems from California through Alaska. Red alder can contribute enormous amounts of N to soils and streams, with published values ranging from 27 kg ha^{-1} y^{-1} (DeBell and others 1983) to 300 kg ha^{-1} y^{-1} (Newton and others 1968). These input rates compare with the atmospheric deposition of N in the region of less than 5 kg ha^{-1} y^{-1} (Johnson and Lindberg 1992). Under these high-N conditions, it is likely that P or some other element delivered by salmon may be of greater ecological significance than N. Increasing densities of salmon should alleviate P limitation faster than N limitation because of the low N:P ratio in salmon carcasses; in some cases, it might actually cause some systems to switch from a P-limited state to an N-limited state. In systems where N loading from watersheds is substantial, this switch may never be reached.

Lag times and Legacies in Ecosystems

The wide distribution of ^{15}N in and along salmon streams reveals little about the ecological impact that MD-nutrients have on the structure and function of streams and riparian zones. Besides possible false signals of ^{15}N from other sources and processes, the mere presence of MD-nitrogen does not necessarily mean that the ecosystem is behaving any differently than an ecosystem that does not receive this subsidy. There are so few data available (approximately eight studies in total, half of which are yet to be published) on ecosystem-scale alterations that caution is advised in extrapolating these findings throughout the salmon-producing region of the Pacific Northwest. Likewise, even though MD-nutrients appear to alter the productivity and composition of stream, riparian, and soil communities, the stability of these communities could be such that the relatively recent decline in salmon populations may not be fully expressed in the respective communities. For example, soils often appear to be deeper along salmon streams, although we have not been able to demonstrate differences in the depths of the O and A horizons in stream sections with and without salmon in southwestern Alaska (K. Bartz and R. J. Naiman unpublished). The mass of accumulated MD-nutrients in the soil or vegetative communities is such that it may take decades before a change is detected. Similarly, internal cycling of nutrients that have accumulated over decades to centuries may support current primary production in lakes and streams. It is possible that the long-term degradation of this nutrient pool due to reduced salmon populations has yet to be expressed in nursery systems throughout the range of Pacific salmon.

Research Frontiers

There are five research issues that, if adequately resolved, could substantially advance our general understanding of the factors that influence salmon population dynamics and the freshwater ecosystems supporting their reproductive and early life history requirements. These research issues include the effects of large-scale environmental change, the responses of riparian vegetation to fertilization by MD-nutrients, and the goal of deciphering the complexity of systems with multiple interactions across broad spatial and temporal scales.

Long-term Effects of Climate Change

Further exploration of the effects of climate change on Pacific salmon and their role in supplying nutrients and energy to freshwater ecosystems should be a major research priority. At present, we have only a weak understanding of the natural modes of climate variability and how it affects ecosystem properties relevant to salmon ecology in both freshwater and marine systems. Climate-related factors, such as hydrologic and thermal regimes, influence the spatial distribution of salmon at both local and continental scales. It is unknown how interdecadal variability associated with regime shifts (Mantua and others 1997) will interact with gradual climate change to control the biological productivity of the North Pacific Ocean and therefore the ultimate potential for MD-nutrient subsidies to freshwater and riparian ecosystems.

Contaminants Carried in Salmon Bodies (Pesticides, Heavy Metals)

The past several decades have seen an increase in the release of pesticides, heavy metals, and other contaminants throughout the world, some of which

bioaccumulate in apex predators. These pollutants are often carried long distances from the point of application by atmospheric and oceanic currents. It is not known if returning salmon carry sufficient contaminants to negate the positive benefits of MD-nutrients to the naturally oligotrophic spawning and rearing sites. However, it has been established that anadromous fish returning to spawn in waters perceived to be nearly pristine do carry contaminants acquired from the ocean (Ewald and others 1998). This raises two important questions: What is the magnitude of contaminant contributions in returning adult salmon to the contaminant budgets of aquatic ecosystems? What are the community- and ecosystem-scale effects of their release into aquatic and riparian systems?

Salmon accumulate nutrients, organic contaminants, and heavy metals from across the broad expanse of the North Pacific and then release them in a relatively confined area associated with freshwater spawning and rearing. For example, in the Copper River of Alaska, anadromous sockeye salmon transport relatively high concentrations of PCBs and DDT from the Pacific to freshwater ecosystems more than 400 km from the coast (Ewald and others 1998). This transport of contaminants results in concentrations in resident grayling (*Thymallus arcticus*) that are twice as high in a lake with access to salmon than in a lake that receives contaminants only via atmospheric loading. Long-range transport of contaminants by anadromous salmon represents an intriguing twist on the ecological roles of these organisms in freshwater and riparian systems, since much of the mass transported to streams by salmon enters aquatic or terrestrial food chains via the direct consumption of flesh and eggs, and there is a good possibility that the transfer of contaminants is more efficient via this pathway than through atmospheric deposition.

Riparian Responses to MD-nutrient Fertilization

Research conducted to date on the effect of MD-nutrients on riparian vegetation provides only a cursory understanding of the ecological consequences of this flux. Key research issues in this area include MD-nutrient distributions in relation to site geomorphology; the delineation of pathways for the transfer of essential MD-nutrients; the linkages among tree growth, ^{15}N content, and salmon escapement; and the effects of nutrients other than N.

There are several pathways for the transfer of MD-nutrients from streams to riparian vegetation: by salmon predators, by floods, by hyporheic flows, and by direct root transfer between plants. Current research suggests that floods and hyporheic flows may not be major pathways of MD-nutrient transport. However, the importance of these processes has not been evaluated at sites with extensive hyporheic zones or where spawning occurs at times when flood flows are common. Under optimal conditions, these pathways may play a more significant role in lateral distribution. Predators and scavengers—especially bears, otters, bats, and gulls—appear to move large amounts of MD-nutrients a substantial distance into the terrestrial environment. However, upslope transfer of MD-nutrients between plants has never been measured. It is known that mycorrhizal fungi associated with roots have the ability to do this for limiting nutrients, but this process has never been addressed in riparian vegetation (Smith and Reed 1997). It is conceivable that, over years to decades, mycorrhizal transfers could account for the MD-nutrient signatures detected in vegetation hundreds of meters from streams. Nevertheless, there are so few studies of MD-nutrient pathways into riparian zones that the issue remains largely speculative, and findings will likely vary with local topography and by element.

We now know that MD-nitrogen in southeast Alaska can increase the growth rate of Sitka spruce nearly threefold. This observation offers several unique and important research opportunities. Can the amount or concentration of MD-nitrogen in individual tree rings be used to reliably estimate the number of adult salmon returning to spawn in the year the ring was formed? Is tree growth related to the number of fish spawning in the previous year, or is the growth related to the accumulation of N from several previous years? If these questions can be answered with reasonable certainty, then it becomes possible to use tree rings to estimate the size of historic spawning runs in individual rivers based on tree growth or [^{15}N] in the rings (Drake and others, forthcoming).

Effects of MD-nutrients on Terrestrial Organisms and Watershed-scale Biodiversity

This review has focused on the importance of MD-nutrients to fresh waters and riparian vegetation. However, there are other organisms that make use of MD-nutrients at critical times in their life cycle. Brown bears and bald eagles (*Haliaeetus leucocephalus*) utilize MD-nutrients immediately before hibernation or before making long migrations. River otters (*Lutra canadensis*), mink (*Mustela vision*), gulls, and other animals utilize these nutrients just before a long winter with limited food resources. The timing of lactation in mink has been shown to vary regionally along the north Pacific Coast of North

America, coinciding with the arrival of salmon (Ben-David and others 1997). The indirect effects of declining salmon populations on these and other animals are suspected to be profound in terms of survivorship, fecundity, ability to compete, and other life history requirements. Unfortunately, there are few data to document indirect effects on the vitality of animal populations that rely on MD-nutrients for nutrition.

COMPLEXITY AND RESILIENCE IN SALMONID ECOSYSTEMS

A more comprehensive understanding of the effects of the full suite of elements contributed by salmon is needed too. In addition to N and P, salmon carry high concentrations of many biologically important elements, and the ecological significance of these elements are poorly understood at best. These elements contribute to a rich array of slow and fast processes underpinning the sustainability of salmon-related aquatic and riparian systems (for example, phytoplankton turnover, soil development, and community structure). Are these components short-term or long-term responses to escapement? How strong or complicated are the internal linkages, and what level of resilience do they provide to external disturbance or declining salmon stocks? How does time of reproduction (summer versus autumn or winter spawning) affect the system-level retention of MD-nutrients? These issues have important resource management implications, especially for determining the appropriate densities of spawning salmon.

In the Pacific Northwest, there is increased interest in modifying salmon management practices to ensure that there are a sufficient number of spawning fish for the nutrient and organic matter subsidies they provide (Larkin and Slaney 1997; Michael 1995; Gresh and Others 2000). However, we have relatively little information from which to determine this level. Stable isotope analysis has been suggested as one method of determining "system saturation" with MD-nitrogen (Bilby and others 2001). However, only streams where coho are the sole salmonid species have been evaluated, and saturation was determined by examining the level of MD-nitrogen in the muscle tissue of juvenile salmon. If this technique is to be used, we will need a better understanding of the dynamics of nutrient cycling and storage at sites where multiple species of salmon spawn. In addition, the responses of other system components (such as periphyton, invertebrates, terrestrial vegetation, and wildlife), as well as the ecological importance of nutrients other

than N, require further study before the appropriate levels of spawning salmon needed to meet the nutritional demands of the watershed can be estimated reliably.

Collectively, responses to these questions and issues will greatly assist in understanding the complexity underlying the dynamics of salmon-related ecosystems. This understanding has direct implications for resource management in terms of creating effective regulations and guidelines that treat the watershed as an integrated salmon-producing system. If the freshwater portion of the salmon production system is to be sustainable, it will require a holistic management approach that treats climate cycles, salmon, riparian vegetation, predators, and MD-nutrient flowpaths and system feedbacks as an integrated system. The long-term sustainability of salmon ecosystems requires that salmon escapement and wildlife harvests be set at levels that ensure an adequate supply and distribution of MD-nutrients. Additionally, riparian management policies need to be developed to effectively protect ecological interactions between the stream and the terrestrial environment in light of long-term environmental variability. These goals represent major challenges for management, as well as a challenge to science to provide the information in a useful manner.

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