

Pacific Salmon in Aquatic and Terrestrial Ecosystems

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Salmon runs in the Pacific Northwest have been declining for decades, so much so that many runs are threatened or endangered; others have been completely extirpated (Nehlsen et al. 1991). This "salmon crisis" looms large in the public eye, because it has serious and wide-ranging economic, cultural, and ecological repercussions. Billions of dollars have gone into industrial and agricultural projects that alter regional rivers in ways that, often unintentionally, make them inaccessible or unsuitable for salmon. Recently, billions more have been spent in largely unsuccessful attempts to restore the languishing salmon runs (Lichatowich 1999). Moreover, enormous nonmonetary resources have been expended in assigning and denying responsibility for failed runs and debating the possible efficacy of various remedies.

As resources that are devoted to reversing declining runs of salmon have increased, scientists and resource managers have been expanding our understanding of the ecological role of salmon and other anadromous fishes, which return from the sea to spawn in fresh water. We have known for years that spawning salmon serve as a food resource for wildlife species (e.g., Shuman 1950) and, when they die after spawning (as most Pacific salmon do), their carcasses provide nutrients (e.g., carbon [C], nitrogen [N], phosphorus [P]) to freshwater systems (e.g., Juday et al. 1932). More recently, scientists have documented that these "salmon-derived nutrient" subsidies may have significant impacts on both freshwater and riparian communities and on the life histories of organisms that live there (Willson et al. 1998, Cederholm et al. 1999).

Because of the burgeoning interest in salmon, growing indications of their ecological importance, and recent calls for management to consider the role of salmon in aquatic and terrestrial ecosystems (e.g., Larkin and Slaney 1997), we take this opportunity to review what is understood about the function of salmon as key elements of ecological systems. Our objectives are twofold. First, we expand on previous reviews of

PACIFIC SALMON SUBSIDIZE FRESHWATER AND TERRESTRIAL ECOSYSTEMS THROUGH SEVERAL PATHWAYS, WHICH GENERATES UNIQUE MANAGEMENT AND CONSERVATION ISSUES BUT ALSO PROVIDES VALUABLE RESEARCH OPPORTUNITIES

salmon (Willson et al. 1998, Cederholm et al. 1999) to include recent research that has amplified and modified earlier ideas about the contribution of salmon to ecosystem processes. In doing so, we describe the composition, magnitude, and distribution of marine inputs to freshwater and terrestrial systems via salmon. We use an expanding group of studies pertaining to stream nutrient budgets and salmon physiology to construct a schematic that illustrates salmon-derived products and the pathways by which they enter and are retained in aquatic and terrestrial food webs. We then consider the ecological variation associated with salmonid ecosystems and how this may influence the ecological response to the salmon input. Second, we consider how this variation in ecosystem response may influence management and conservation efforts.

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We conclude by suggesting new research directions to help fill the gaps in our current understanding of salmonid ecosystems.

The salmon input

We focus on five species of Pacific salmon that spawn in freshwater systems of North America: chinook (*Oncorhynchus tshawytscha*), sockeye (*O. nerka*), pink (*O. gorbuscha*), chum (*O. keta*), and coho (*O. kisutch*). All five species share a general life history: Adults return to freshwater, usually in late summer and fall, where they cease feeding, spawn, and die. After some months, young emerge from the gravel in early spring and, depending on the species, spend up to 2 years in freshwater habitats before migrating out to sea. The fish remain at sea for 1 to 7 years, feeding and gaining over 90% of their biomass, before returning to fresh water to complete the cycle (Groot and Margolis 1991).

Composition. When salmon enter fresh water, they have stored nearly all of the energy necessary for upstream migration and reproduction, but the magnitude of resource reserves varies greatly among populations, often in accord with the length of upstream migration (Brett 1995, Hendry and Berg 1999). For example, chum salmon in the Yukon River may spawn near the mouth or nearly 2000 kilometers (km) upriver. The difference in chemical composition of "upriver" versus "downriver" spawning salmon is so large that it was suggested as a metric to separate the stocks that are harvested in a mixed-stock fishery on the coast (Brett 1995).

As salmon migrate and approach spawning areas, their body composition changes dramatically. Both males and females store much of their lipid throughout the visceral and soma tissue, particularly in the muscle, skin, and skeletal tissue (Hendry and Berg 1999, Gende 2002). Stored lipids fuel migration to spawning grounds, which results in loss of some of the energy to metabolic heat en route and produces carbon dioxide and water as waste products. Females use some stored lipid for production of eggs, which can constitute more than 20% of body mass, whereas males tap both lipid and protein reserves to develop secondary sexual characteristics (Hendry and Berg 1999). Once on the spawning grounds, fish use most of the remaining lipid to fuel spawning activities such as excavating and defending redds (females) and fighting for access to females (males). Body tissue proteins also are used as an energy source, resulting in endogenous nitrogen excretion in the form of ammonia (and some urea), primarily across the gill membrane (Wood 1995). The length of time fish live on the spawning grounds varies depending upon the population (generally less than 3 weeks). Although a large fraction of the lipid and protein has been metabolized or deposited in the gravel as eggs, carcasses may contain up to 16% protein and 3.5 kilojoules per gram wet mass of energy (Hendry and Berg 1999, Gende 2002). Other forms of N, such as collagen in the skin, may not be depleted and remain within the carcass.

Salmon also contain macroelements, that is, minerals found in large amounts (Robbins 1993), such as potassium

and calcium (Ca). Although salmon lose calcium phosphate during migration, which allows bone tissue to turn into cartilage necessary for the formation of secondary sexual characteristics, total body Ca and P do not decline precipitously during freshwater migration and spawning (at least for pink and chum salmon populations that spawn in small coastal streams; Gende 2002). Phosphorus, stored chiefly in the bone, muscle, and male gonads, makes up less than 0.5% of the body mass, but may be an important input when considering the large numbers of fish entering streams and lakes (Donaldson 1967). Few studies have quantified the macroelement content of the fish, but clearly it may play a role in the nutritional quality of salmon for consumers; for example, some minerals are necessary in small amounts for health and growth (Robbins 1993).

Magnitude. The flux of salmon biomass entering fresh water from the ocean can be massive. A large run of 20 million sockeye (to the Bristol Bay region, for example) can yield as much as 5.4×10^7 kilograms (kg) of biomass, which equates to 2.4×10^4 kg of P, 1.8×10^5 kg of N, 2.7×10^5 kg of Ca, plus other macroelements. Fish commonly migrate up large rivers and disperse into tributaries. Thus, the density of fish in tiny coastal streams with small numbers of spawners may equal or exceed that in tributaries of major rivers that host larger absolute numbers of fish.

The number of fish entering a system also varies temporally at several scales. Over past centuries, salmon abundance has varied dramatically in relation to geological changes in the land and changes in ocean conditions (Francis and Hare 1994). Ocean conditions that influence primary productivity in the North Pacific oscillate over a multidecadal cycle (Mantua et al. 1997) and probably affect the growth and survival rates of salmon (Gargett 1997). Natural variations also occur over shorter time intervals of a few years, in response to differences in precipitation and stream flow, diseases, and population feedback mechanisms. Since the onset of industrial fishing in the 1800s, the number of fish returning to a system is also heavily contingent upon harvest levels (Finney et al. 2000), with some stocks suffering 90% mortality and others with 5% or no mortality (Templin et al. 1996).

Distribution. Historically, streams on both sides of the North Atlantic (including the Mediterranean) and the North Pacific supported strong runs of anadromous salmon. Climate and landscape changes through geological time wrought habitat changes that periodically extinguished local populations, but residual populations recolonized habitable streams or established populations in newly accessible rivers. More recently, anthropogenic changes have destroyed many of the runs (Lichatowich 1999) and decreased spawning area by changing stream habitats. As a result, these changes reduced the influx of salmon to streams and, by reducing the source populations, diminished the chances of recolonization.

In natural conditions, the enormous load of salmon nutrients (C, N, P, etc.) is distributed upstream as far as suitable

habitat is accessible. Thus stream systems serve as conduits for the input of ocean-derived materials to freshwater and terrestrial systems. In a large watershed, salmon enter smaller and smaller tributaries until they are dispersed throughout the watershed, sometimes into tiny headwater streams far into the interior (figure 1a). For example, fish entering the Columbia River historically dispersed as far as Redfish Lake, Idaho, a migration of over 1000 km with an elevation gain of over 2000 meters (m) (Groot and Margolis 1991, Gross et al. 1998). Smaller coastal watersheds usually receive fewer fish, but there are thousands of smaller streams throughout the landscape (figure 2). Although most nutrients are deposited near the stream, most mobile consumers are close to salmon streams. For example, the Tongass National Forest, encompassing almost all of southeastern Alaska, contains nearly 5000 salmon-supporting streams (Halupka et al. 2000); consequently 47% of the forested area within the Tongass falls within 0.5 km of a salmon stream and over 90% within 5 km (Willson et al. forthcoming). The influx of anadromous fish effectively extends the interface between ocean and land, thereby expanding the surface area over which ecological exchanges take place.

Once salmon arrive at spawning streams, their nutrients are spread still more widely over the landscape by the activities of terrestrial consumers and water movements. For example, bears congregate at streams to catch salmon and often drag the carcasses into the riparian forest, where they are partially consumed (Gende et al. 2001a). Bears foraging at streams in British Columbia move 58% to 90% of all salmon biomass to land, sometimes hundreds of meters from the stream (Reimchen 2000), and further distribute the minerals and nutrients in the form of urine and feces as they move throughout the riparian and upland forests (Hilderbrand et al. 1999a). Stream insects feeding on salmon carcasses often have aerial adult phases, during which they can fly far from the natal streams. Avian scavengers remove chunks of salmon tissue and carry them onto land and also leave their excretory products across the landscape. In addition, the porous gravels and mobile channel beds characteristic

of spawning streams provide areas beneath and beside the surface channel where water flows back into the subsurface saturated zone (i.e., the hyporheic zone; Edwards 1999). Products of salmon decomposition move with this water, transferring large amounts of salmon-derived N and P to adjacent riparian zones 70 m or more from the spawning stream channel (O'Keefe and Edwards forthcoming).

After spawning, an unknown proportion of the salmon input is exported and remobilized as stream currents continually carry carcasses and decomposition products back downstream toward the ocean. A fraction of the input is also lost as outmigrating smolts (e.g., Gross et al. 1998, Lyle and Elliott 1998), many of which die while at sea. Therefore, mechanisms of salmon-nutrient retention become important by retarding that loss and making nutrients available to other organisms over a longer time span. For instance, many plant species grow rapidly in the spring and early summer, whereas the bulk of salmon runs occur in late summer to early fall. Without mechanisms to store nutrients over winter, there would be little stimulation of total annual primary productivity by salmon-derived inputs.

Retention mechanisms vary with latitude, climate, animal populations, vegetation cover, and stream geomorphol-

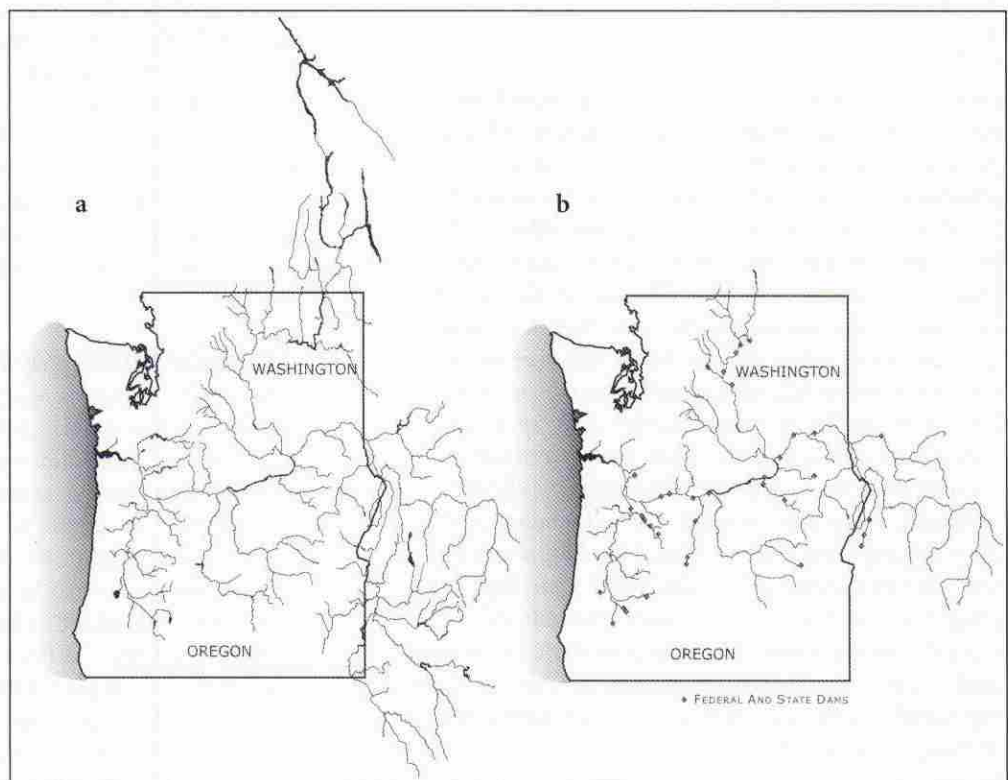


Figure 1. (a) Predevelopment pattern illustrating how migrating and spawning salmon effectively extend the influence of oceanic productivity to freshwater systems by migrating far into the continental interior through a large river system. As fish move through the mainstem to spawning grounds, their biomass is widely distributed throughout the landscape, and ecosystem nutrient inputs (per square meter) may actually increase toward the low-order (headwater) reaches. (b) Truncation of marine-derived nutrient distribution caused by dams and habitat destruction.

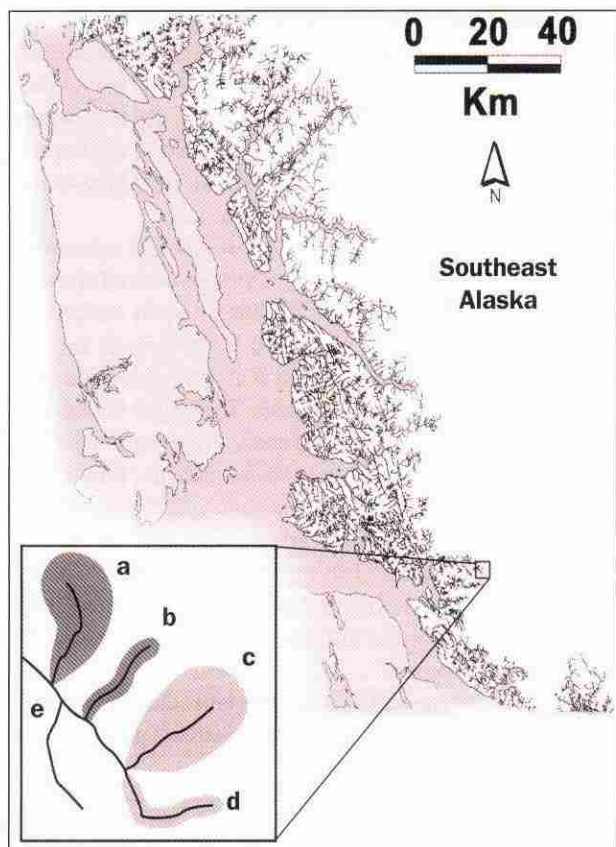


Figure 2. Penetration of salmon-bearing coastal streams into the continental margin within a section of Tongass National Forest in southeastern Alaska. Although streams are shorter and runs are smaller (in absolute numbers) than under historic conditions in large interior rivers, the high drainage density ensures that marine inputs are distributed widely within much of the coastal forested regions. Southeast Alaska has over 5000 salmon streams; initial estimates have found that over 90% of this forested area falls within 5 kilometers (km) of a salmon stream. Inset: Representation of the spatial pattern of reduction of marine inputs to the terrestrial ecosystem caused by different anthropogenic effects: (a) intact stream ecosystem; (b) normal salmon escape-ment but impaired transfer caused by elimination of bears or other predators or reduction in hydrologic coupling; (c) intact transfer mechanisms but reduced run size caused by obstructions, habitat degradation, overfishing, and so on; (d) loss of transfer mechanisms and run reductions; and (e) run extirpated with or without impairment of transfer mechanisms.

ogy. In forested regions, fallen trees in streams create physical barriers that retain carcasses (Cederholm and Peterson 1985) and pools where carcasses accrue and decompose or become buried in the stream substrate. Direct consumption by predators and scavengers also stores the biomass as consumer tissue. Within northern streams, freezing may also be a significant retention mechanism by locking carcasses in

the ice and snow where they can be an important food source for scavengers during winter or the following spring (e.g., Hansen 1987).

Biofilms on sediment surfaces are another potential site for storage of salmon-derived nutrients. Inorganic forms of N and P and dissolved organic matter (DOM) are rapidly taken up into the matrix of algae, bacteria, fungi, protozoans, and nonliving organic matter that make up biofilms (Freeman and Lock 1995). DOM leaching from salmon tissue is rapidly sorbed onto stream sediments (Bilby et al. 1996). Salmon-derived ammonium (NH_4^+) and phosphorous moving into a hyporheic zone within a stream in southwestern Alaska were removed within the first few meters of subsurface flow (O'Keefe and Edwards forthcoming), presumably within biofilms on the sediment surface. Storage within biofilms for weeks or months, followed by mineralization and reintroduction into the flowstream, are potentially important mechanisms by which marine-derived N and P could become available to surface algae during the following growth season.

Hyporheic flows extending several hundred meters into riparian floodplain forests have been documented in salmon streams, which creates an enormous potential storage volume (Clinton et al. 2002). Hyporheic zones contain much greater epilithic surface area than surface benthos (Edwards 1999) and exist largely below the flood-scour depth. Thus, hyporheic storage is probably a large, although poorly quantified, storage area of salmon-derived nutrients.

In small coastal streams, many carcasses may be flushed back into the ocean, or spawning may occur in the intertidal zone. Estuarine algae can take up the salmon-derived nutrients, however, thereby feeding copepods that are in turn fed upon by juvenile salmon, all of which serves as a positive feedback mechanism for salmon production (Fujiwara and Highsmith 1997).

Dispersal pathways

Although it is common to refer to salmon-derived nutrients as if they were a uniform pool, the ecosystem effects of materials derived from salmon vary greatly with their chemical form relative to various consumer's needs. Confusion over the "importance" of salmon to lakes, streams, and forests has arisen, in part, because of the failure to distinguish the two broad types of pathways by which salmon tissue is incorporated into terrestrial and freshwater ecosystems: (1) direct consumption of salmon as food, by which "input" passes up the food chain in fairly predictable steps, and (2) recycling of the products of decomposition, leaching, and excretion, which move through a variety of less well-studied pathways. Figure 3 illustrates those consumption and recycling pathways schematically over the consumption and decay sequences. The vertical axis represents time, starting with the entry of salmon into spawning areas (early), progressing to more spawning and residence time on beds (mid), continuing to the end of spawning when dead and dying fish dominate (late), and finally ending with the postspawning period, when remaining carcasses are processed. The progression of the fish along the time

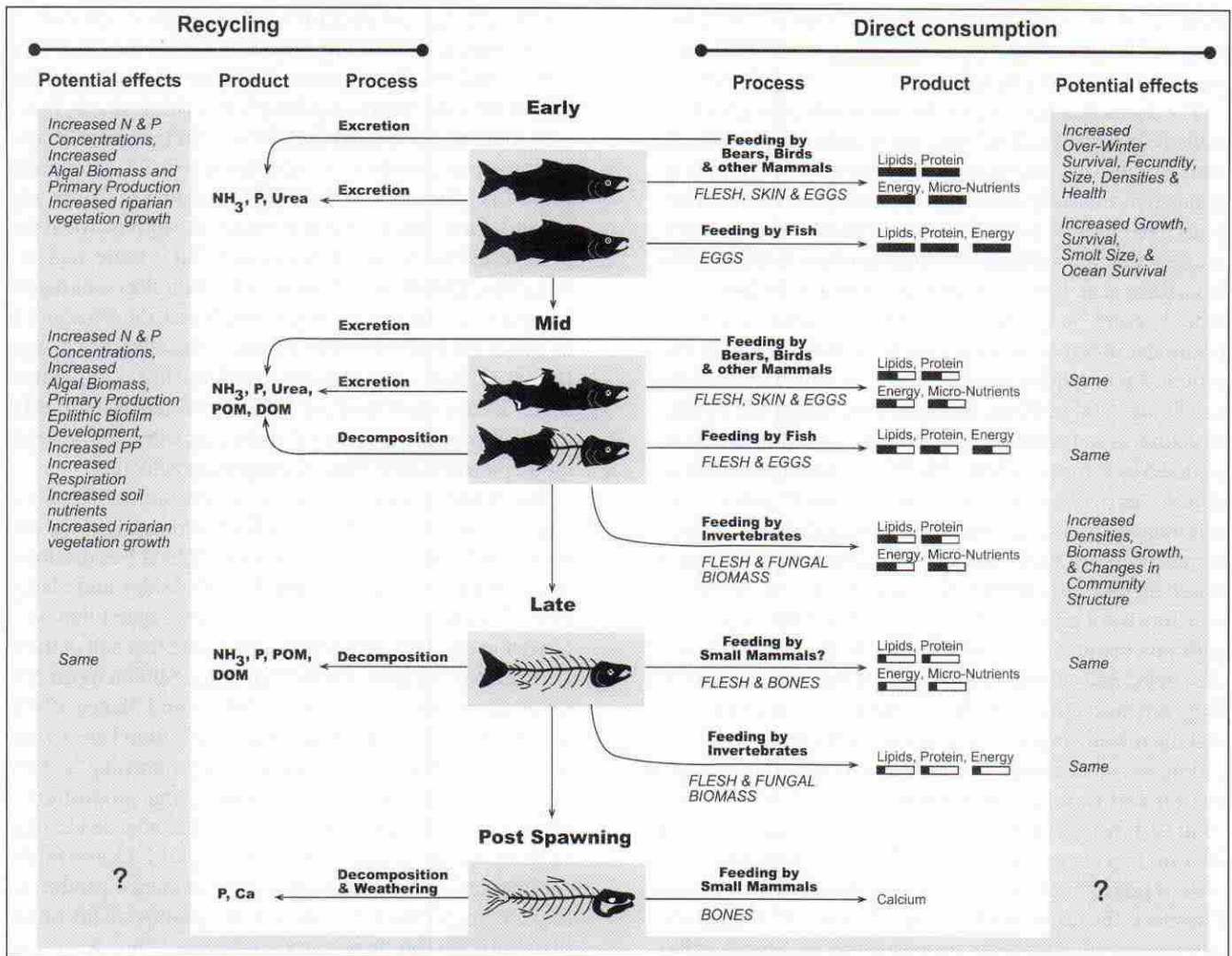


Figure 3. Schematic of major dispersal pathways for salmon-derived materials during the course of spawning. On the left is the “recycling” pathway and on the right is the “direct consumption” pathway. Boxes beneath the derived products of feeding pathways suggest changes in the importance of various components as spawning progresses and tissue chemistry and consumers change. Relative proportions are not to scale; they are simply suggestive of trends.

series varies with species, location, and physical factors such as hydrology.

The left side of the diagram represents recycling pathways that are dominated by excretion and decomposition and mediated by invertebrates, fungi, bacteria, and physical processes. These processes embody what are commonly termed “bottom-up” effects influencing ecosystem processes via plant or biofilm production. The right side of the diagram represents consumption pathways by which salmon biomass is incorporated into trophic webs directly via feeding. Salmon nutrients can enter the food webs at many trophic levels because of the omnivorous nature of many stream and terrestrial biota. Consequently, the right side cannot be easily characterized by a directional flow of salmon biomass (e.g., top-down or bottom-up), confounding any simplistic view that these systems are regulated by one or the other (see also Power 1992).

The exact nature of the salmon-derived material entering the food web varies at different stages in the decomposition cycle of the salmon. For example, on the recycling side of the

diagram, the first inorganic nutrient supplied to stream water by salmon is NH_4^+ excreted by living fish before spawning mortality begins (O’Keefe and Edwards forthcoming). A week or two later, levels of ammonium and soluble reactive phosphorus (SRP) in stream water further increase, probably leached from carcasses or gametes released during spawning activities. As salmon continue to die and biomass from the carcasses is processed by consumer or microbial activity, SRP and NH_4^+ increase but then decrease as the number of fish in the stream declines (e.g., Brickell and Goering 1970, Sugai and Burrell 1984). Finally, when only the skeletal tissue remains, P and Ca in the bones are the primary nutrients left. On the consumption side of the diagram, predators such as bear or otter (or other vertebrates large enough to capture live, ripe adult salmon) feed on lipid-rich living fish in the early stages of the spawning cycle, but as spawning progresses, feeding by scavengers on eggs, carcasses, and “leftovers” increases. As the spawning run progresses and most fish have depleted much of their energy, the average energetic “re-

ward" of tissue consumption decreases (Gende 2002). Insects and fungi may take increasing amounts of salmon tissue as the number of carcasses increase (e.g., Reimchen 2000).

The distinction between the two dispersal pathways is particularly important with reference to the techniques commonly used to infer the importance of salmon-derived inputs at population and ecosystem levels. For example, a common approach has been to use stable isotope signatures to quantify transfer of salmon nutrients to various consumers and biofilms (e.g., Kline et al. 1997). The large difference in the heavy isotope (^{15}N and ^{13}C) composition of salmon tissue relative to freshwater or terrestrial values has been used to estimate the proportion of salmon-derived N or C in animal tissues, invertebrates, and biofilms. Nitrogen flow within the trophic structure, as indicated by ^{15}N composition of consumers, is assumed by some to also provide information about flows of salmon-derived P. When organisms eat salmon tissue (consumption pathway), the ratio of C, N, and P in fish tissue may be relatively well preserved, making stable isotopes a useful tracer method. In contrast, the original marine elemental signature is not preserved in the excretion and decomposition pathways because C, N, and P are physically and chemically decoupled and subsequently processed by widely divergent biogeochemical processes. For example, N is subject to several microbially mediated processes (nitrification, denitrification, etc.) that can dramatically alter its absolute concentration and isotopic composition (Kline et al. 1997). In contrast, P (which has no stable isotopes) is not subject to loss by conversion to gas but is strongly sorbed to inorganic minerals or precipitated out of solution under some conditions. Therefore, the use of stable isotopes to infer the magnitude of transfers within processes represented on the left side of figure 3, although increasingly used, is poorly documented and highly speculative compared with the consumption pathway. By extension, it should not be assumed that the importance of salmon biomass as food is directly correlated with the importance of inorganic nutrients to bottom-up pathways.

Given such widely divergent pathways, products, and consequences, the term *marine-derived nutrients* is so imprecise as to be useless, except when referring to the general phenomenon of the large influx of marine-originated biomass (in this case salmon, but see also Polis and Hurd 1996). It is important that terms distinguish the specific salmon product, because the importance of different salmon contributions relative to other input sources varies, the mechanisms controlling their uptake and retention are distinctly different, and the type of nutrient that is limiting will vary. Improved understanding would be promoted by more specific terms such as "salmon-derived nitrogen" or "salmon-derived lipids."

Ecological consequences of the input

To assess the biological importance of salmon-derived nutrients, we must know the magnitude, composition, and variability of the input, as well as the specific attributes of the watershed receiving them. For example, within streams, the potential importance of salmon-derived N versus P in sup-

porting primary production varies with the magnitude of other sources. Historically, streams in the Pacific Northwest were considered nitrogen limited because of low nitrogen inputs and the dominance of phosphorus-rich bedrock. However, more recent research has shown that inorganic N concentrations in streams vary widely from 10 to 20 micrograms (μg) N per liter to over 1600 μg N per liter (O'Keefe and Edwards forthcoming), a concentration at which N would not be expected to limit photosynthesis. What is more, high nitrate concentrations are often associated with alder, a nitrogen-fixing tree common in the Pacific Northwest, the distribution of which has been expanded by long-term climatic changes (Hu et al. 2001) and logging practices (Ruth and Harris 1979). Hence, the importance of salmon-derived N may be less than commonly assumed and varies with natural vegetation patterns and human management activities.

In contrast, P concentrations tend to be uniformly low except in areas with P-rich sedimentary bedrock (Ashley and Slaney 1997), and recent work has highlighted P as the dominant limiting nutrient (Bothwell 1989, Ashley and Slaney 1997). Nutrient patterns in Idaho streams suggest that one-quarter to one-half are nutrient limited and that half of those are P limited (Thomas et al. forthcoming). Salmon molar N:P ratios range from 12:1 to 15:1 (Ashley and Slaney 1997), making them relatively phosphorus rich. Within Lynx Creek, Alaska, phosphorus that is imported by spawning sockeye salmon at average run sizes constitutes a large proportion of the P available to epilithon (organic matter attached to rock surfaces) on an annual basis (O'Keefe and Edwards forthcoming) and may be the most important marine product of the recycling pathway. In some systems, however, light, rather than nutrients, limits primary production. Thus, a pulse of salmon-derived nutrients may have little or no effect on primary productivity (Rand et al. 1992), although salmon may still be an important resource for stream or terrestrial biota via the consumption pathway.

Given the heterogeneity in habitats and limiting factors, it follows that the ecological consequences of inputs vary among habitats and with dispersal pathways. Epilithic chlorophyll standing stocks increased following salmon spawning in some studies (e.g., Richey et al. 1975, Wipfli et al. 1998), were unaffected in other studies (Minshall et al. 1991) and decreased after spawning episodes in still other streams (Minikawa 1997). Increases in salmon-derived inorganic nitrogen and phosphorus compounds have been documented from several streams (Brickell and Goering 1970, Schuldt and Hershey 1995, Minikawa 1997), confirming that excretion and mineralization of carcasses does increase the inorganic nutrient capital of some streams. Furthermore, artificially increasing inputs of inorganic P and N in streams in British Columbia increased chlorophyll accrual rates, benthic insect density, and the growth rates and size of fish (Perrin et al. 1987, Johnston et al. 1990, Mundie et al. 1991). Therefore, by inference, it is assumed that nutrients released by spawning salmon also have the same effect. Increased ecosystem primary productivity in streams, as a result of salmon nutrient inputs, remains

an interesting hypothesis that has not been confirmed, however, particularly across a broad range of stream types and spawner densities.

Increased lake productivity that is caused by salmon-nutrient inputs is better documented. Returning sockeye salmon can contribute a large proportion of available P and N, depending upon the size of the salmon run (Hartman and Burgner 1972, Stockner and Shortreed 1975, Mathisen et al. 1988), which may elevate phytoplankton and zooplankton densities and increase juvenile salmon production (Narver 1967). As in stream systems, experimental nutrient inputs to lakes, primarily P, increased lake productivity (Hyatt and Stockner 1985, Stockner and MacIsaac 1996); in contrast, nutrient budgets within Redfish Lake, Idaho, suggest that stimulation of lake production by spawning runs of salmon has always been small, thus indicating that lake responses also vary with geography (Gross et al. 1998).

There is abundant evidence that salmon availability influences population dynamics of consumers via the consumption pathway. More carcasses generally translate into higher densities and elevated growth rates of invertebrates, and juvenile salmonids may grow faster by directly consuming salmon tissue or consuming invertebrates that have been scavenging salmon carcasses (Johnson and Ringler 1979, Bilby et al. 1996, 1998, Wipfli et al. 1998, 1999, Chaloner and Wipfli 2002). Furthermore, juvenile coho salmon had higher levels of whole-body lipids and a higher proportion of lipid allocated to energy reserves (triacylglycerol) when reared in the presence of salmon carcasses (Ron Heintz, National Marine Fisheries Service, Auke Bay, AK, personal communication, 22 September 2002), which may lead to higher survival (Wipfli et al. forthcoming). Additionally, marine isotopes of N and C are higher in several trophic levels in salmon versus nonsalmon streams (Kline et al. 1997), illustrating that these freshwater biota are sequestering marine nutrients into body tissues, presumably by direct consumption of salmon tissue (Bilby et al. 1996).

Similar responses may occur in terrestrial communities. Lower trophic levels, such as invertebrate scavengers (e.g., dipterans), utilize the available salmon biomass (e.g., Reimchen 2000) and reproduce, thereby increasing local densities by conversion of salmon biomass into invertebrate tissue. Densities of many vertebrates increase locally, presumably by moving from surrounding areas to feed on salmon. During the breeding season, insectivorous riparian passerines are found in greater densities on salmon streams than on other streams, suggesting that bird communities may be responding to the pulse of invertebrates produced by the availability of salmon (Gende and Willson 2001). Across the landscape, the carrying capacity of bears increases where salmon are available, with populations up to 80 times denser in coastal areas, where salmon are abundant, than in interior areas (Miller et al. 1997, Hilderbrand et al. 1999b). Fitness-related variables, including growth rates, litter sizes, and reproductive success, have been attributed to salmon availability for salmon consumers, such as eagles, bears, and mustelids, which suggests

that salmon play an important role in the population dynamics of these terrestrial consumers (Hansen 1987, Ben-David 1997, Hilderbrand et al. 1999c).

Terrestrial vegetation also may respond to the presence of salmon. The ^{15}N signal presumed to be salmon-derived has been detected in riparian shrubs and trees up to 500 m or more from streams (Bilby et al. 1996, Ben-David et al. 1998, Hilderbrand et al. 1999a) in Washington and Alaska. Marine signatures are higher in areas where bears feed on salmon (Ben-David et al. 1998, Hilderbrand et al. 1999a), which suggests that the foraging activities of bears play an important role in making salmon-derived nutrients available to terrestrial vegetation. There is also some indication that growth of riparian trees may increase where salmon-derived nutrient input occurs, particularly in areas with bear foraging activity (Helfield and Naiman 2001), although the spatial extent of this phenomenon is unknown. Increased growth of riparian vegetation caused by salmon inputs, if it occurs widely, could have ramifications for riparian systems by changing litter, large woody debris, and the amount of light reaching streambeds, as well as by altering terrestrial vegetation structure (Helfield and Naiman 2001), food for herbivorous insects, and cover for nesting birds.

In addition to the direct effects of salmon subsidies, there are several indirect ecological ramifications of these subsidies. We note three possible examples: (1) Salmon are a major source of food for bears, but bears also consume fleshy fruits and thus serve as important seed dispersal agents for numerous plant species in coastal forests (e.g., Willson 1993). Without salmon, bear densities would be lower and seed dispersal patterns could be altered, with unknown consequences. (2) Fertilization of plants commonly leads to higher nutrient content and enhanced growth, and some herbivorous insects attack fertilized plants at high rates (Price 1991). Birds feed on many herbivorous insects and, in some circumstances, are capable of reducing the herbivore load on plants, thus fostering better plant growth (Marquis and Whelan 1994). Higher densities of insectivorous breeding birds along salmon streams in spring (Gende and Willson 2001) might mean that natural control of herbivorous insects is better in salmon-subsidized forests. (3) Because salmon subsidies can lead to enhanced growth and survival of stream-resident fish (Bilby et al. 1998), life-history strategies that are dependent on juvenile growth rates may change. For instance, the timing and even the probability of migration from fresh water to the sea may vary with juvenile growth rates (Healy and Heard 1984), which in turn affects body size, patterns of spawning competition, and fecundity, with ramifications for population productivity and thus for consumers and commercial harvests.

Conservation and management

It is clear from the growing body of literature that salmon may influence the food webs, trophic structure, nutrient budgets, and possibly the productivity of freshwater and terrestrial systems, although the effect varies widely between systems and is contingent upon timing, scale, retention mechanisms, al-

ternative nutrient sources, and baseline limiting factors. How might these results influence resource managers and conservation practitioners?

The emerging picture of the ecological importance of salmon subsidies to freshwater and terrestrial ecosystems forcefully emphasizes the importance of a broad, holistic perspective. The links between ocean and land mean that management of an ocean fishery can have far-reaching effects on distant ecosystems, and vice versa. Any management activity that reduces the numbers of salmon returning to spawning grounds may influence processes that are driven by the salmon input (figures 1b, 2). Furthermore, those links necessitate cross-disciplinary research and applications of knowledge (Willson et al. 1998). The big picture must be viewed with care, however. Regional and temporal variation in inputs and outcomes means that results from a single study cannot be assumed to be universally applicable. Factors limiting productivity differ among locations. Moreover, the ways in which nutrients are spread and the degree to which they are spread across the landscape vary, even in natural systems. Attempts to reintroduce some single component (e.g., C or N) to a highly complex, failing system run the risk of all simplistic approaches, in that they neglect the inherent complexity of the system.

Furthermore, managers considering the role of salmon should recognize that the ecological response to the salmon subsidy is species specific. Artificially placing a few salmon carcasses on stream banks (or in streams) may locally increase invertebrate populations by several orders of magnitude, as they colonize and reproduce within hours or days of the availability of the carcasses. The same number of carcasses, however, would not permit a population response by larger vertebrates such as eagles, bears, or mustelids (which in turn serve as important nutrient-dispersal agents), because that would require thousands of kilograms of salmon, distributed across many streams, over a long time period.

Emerging management techniques are primarily designed to manipulate processes via the recycling pathway without explicitly considering biomass-related ecosystem flows (via the consumption pathway). For example, in an effort to replace the inorganic minerals reduced by the depletion of salmon runs, companies have produced slow-release fertilizer briquettes that are designed to increase inorganic P concentrations in selected streams (Sterling et al. 2000). Fertilization of streams and lakes with inorganic P and N has successfully increased algal standing stocks, salmonid fry weights, and production (Stockner and MacIsaac 1996, Ashley and Slaney 1997). However, if a significant proportion of the increased salmon numbers produced by such augmentation is not allowed to return, die, and be consumed in the natal waters, the transfer of salmon-derived products to aquatic, and particularly to terrestrial, food webs will remain truncated even if stream and lake productivity is enhanced. If managers see nutrient augmentation solely as a way to increase salmon harvests, rather than as a stopgap measure to enhance runs until densities of adult fish return to a sustainable level (Gresh

et al. 2000), then the decoupling of subsidies to the terrestrial ecosystem will remain. In such a scenario, the failure to distinguish salmon as food from salmon as inorganic nutrients could result in unbalanced management practices.

A broad perspective carries an ecological message for fisheries management, which is driven chiefly by commercial considerations and the goal of harvesting as many fish as possible. What is "possible" has been altered during the course of commercial exploitation, from "taking everything that could be caught" to the concept of "maximum sustainable yield" (Smith 1994). Even that concept has been questioned, however, because uncertainty in estimating fish population dynamics makes prediction of sustainable harvest levels very difficult (Hilborn and Walters 1992). Most recently, the ecological value of salmon subsidies has attracted management attention, chiefly for enhancing fish production. Yet to be achieved is inclusion of the wider ecological significance of salmon for the landscape. Small stocks are ecologically important as sources for colonizers, food for wildlife, and nutrients for freshwater and terrestrial systems, but they are rarely counted and sustain unknown levels of harvest because of mixed-stock fisheries. Small stocks also increase genetic variation, which is important in maintaining evolutionarily significant units.

A primary goal of conservation and restoration is obviously the conservation or restoration of the salmon runs themselves, because without them, none of the related processes operate. To this end, efforts at enhancing stream productivity, water quality, natural water flow patterns, and stream accessibility and suitability are all appropriate. In addition, the broad perspective provides new goals for conservation and restoration efforts by drawing attention to the ecological roles of salmon subsidies. Restoration of fully functional systems clearly depends on inclusion of the means of spreading the salmon subsidies across the landscape, via surface and hyporheic flows and populations of consumers (figure 2b). In some regions, full restoration is clearly impossible, because changes in animal habitats, hydrology, and stream geomorphology have permanently altered ecosystem function. In these cases, the systems may suffer from one (or more) of the "ratchets" described by Pitcher (2001), for example, human-caused species extinction, that prevent systems from returning to their natural state. In other regions less altered by human activity, full maintenance of natural ecosystem function may be possible. Of particular importance is the preservation and understanding of the processes in relatively pristine systems, so that they can provide a baseline goal toward which restoration efforts can be aimed. In so doing, another ratchet can be avoided, for example, a sliding scale of what is perceived as natural, caused by a lack of true reference systems (Pitcher 2001).

Future research

It is clear that salmon-derived nutrient subsidies can play a significant role in the ecology of aquatic and terrestrial ecosystems, but site- and taxon-specific variability influence the

magnitude of the response. For fisheries managers to accept the concept that salmon escapements should be managed to maximize ecosystem productivity and then to translate that concept into improved management, researchers must first provide some estimates of the relationship between the number of fish allowed to escape commercial harvest and return to spawn and basin-specific intrinsic factors and productivity. More research is required on dose-response relationships where varying spawning densities lead to predictable ecosystem responses. For example, there is evidence that the ecological response varies with the density of available carcasses. In Alaska, NH_4^+ and SRP concentrations varied predictably with run size (O'Keefe and Edwards forthcoming), and biofilm and benthic macroinvertebrate standing stocks appeared to reach an asymptote at intermediate levels of carcass availability (Wipfli et al. 1998, 1999). Presumably above some level of food availability or mineral input, other processes limited production.

To our knowledge, the only attempt to consider the ecological effects of salmon spawners while establishing escapement goals was by Bilby and colleagues (2001), who proposed using the stable isotope signature of stream fish. They observed that tissue ^{15}N values reached an asymptote in juvenile coho salmon as escapement levels increased, suggesting that coho fry might be used to define the point at which the (freshwater) ecosystem is saturated by spawners. Although the usefulness of their approach has not been broadly confirmed, it challenges other scientists to develop additional approaches to translate our emerging understanding of the ecological effects of salmon-derived nutrients into practical management techniques.

The role of salmon in influencing ecosystem productivity needs clarification. Despite the conventional wisdom that spawning salmon increase aquatic ecosystem productivity, only one published study has quantified primary productivity (g per m^2 per day) in response to the presence of spawners. The sole reference documenting an increase in primary productivity in streams (Richey et al. 1975) was for landlocked kokanee salmon, and results from that study also showed that the response varied widely with run size and stream flow. We know of no study in which secondary production by stream invertebrates has been quantified. Most publications report indirect responses such as increases in density, standing stocks, or individual growth rates. Although such surrogates may be correlated to ecosystem productivity, the relationship is not necessarily direct or consistent throughout the range of salmon or over time. Although it is intuitively appealing to assume that such evidence suggests that productivity is enhanced, studies confirming such productivity have not been done.

The influence of salmon-derived inputs on biodiversity is largely unknown, because baseline levels of productivity and the relationship between biodiversity and productivity may vary among sites. For example, the relationship between diversity and productivity was initially thought to be hump-shaped: Diversity increases with productivity at lower levels

of productivity but decreases as productivity continues to increase (e.g., VanderMeulen et al. 2001). If that relationship applies to systems subsidized by salmon, then the outcome for diversity clearly depends on the initial levels of productivity. An increase of diversity would be predicted only if the initial levels of productivity were relatively low. However, recent research has suggested that this relationship varies among sites and taxa (Mittelbach et al. 2001, Schmid 2002). An additional consideration is that increased productivity may permit increases of population size, thus lowering the risk of extinction and buffering biodiversity through time. Although there is some evidence of salmon influencing biodiversity or community structure of invertebrates (Piorkowski 1995), the relationship between biodiversity and productivity in salmon-subsidized systems has yet to be established in a comprehensive manner.

The validity of using stable isotope techniques to track salmon biomass throughout receiving ecosystems requires confirmation. Carbon and nitrogen isotopes have been used extensively to study the role of salmon in aquatic and terrestrial ecosystems; these heavy isotopes can be traced only by making many assumptions about competing processes and alternative isotopic pool signatures, however (Kline et al. 1997). As yet, little work has tested the validity of those assumptions or how other factors may influence isotope signatures, including fractionation rates among trophic levels, vegetation patterns (e.g., the role of nitrogen-fixing alder), and the changes in isotopic signatures of salmon (Doucett et al. 1999). Recent work in southwestern Alaska has shown that denitrification potentials are greater in spawning streams than in reference streams without salmon (Gilles Pinay, Université de Rennes I, Rennes, France, personal communication, 15 November 2001), which suggests that there are systematic violations of some key assumptions in using ^{15}N values to trace marine N. Even where underlying assumptions are valid, the ecological relevance is not clear when, for example, stream biofilm has 45% of its N derived from salmon, especially in P-limited ecosystems.

Long-term, whole-system manipulations are necessary to quantify dose-response relationships and to avoid experimental design flaws in current approaches (see also Schindler et al. 2000). Published research is largely descriptive, not experimental, and tracking the fate of salmon biomass within ecosystems is difficult because of uncontrolled and poorly quantified confounding factors. The value of nonsalmon reference streams as controls is weakened by potential systematic bias, and the difference in dispersal pathways between nonliving and living fish limits the generality of small-scale fish-addition experiments. Detailed study of systems where escapements are dramatically altered, either by reducing existing runs for prolonged periods or by studying run introductions in areas where fish passes have been constructed, would assist the pursuit of the previously suggested research elements and would clarify our interpretation of existing data.

Finally, we have focused on the role of Pacific salmon in the Pacific Northwest because most of the information on salmon inputs to freshwater and terrestrial ecosystems comes from work on Pacific salmon. But anadromy is not unique to the Pacific Northwest nor to salmon; other species with anadromous life histories include smelt, sturgeon, noodlefish, and lamprey. Anadromy is widespread in the temperate and boreal regions of the Northern Hemisphere (McDowall 1988), and there are some reports that consumers respond to the subsidies provided by some of these species (e.g., Gende et al. 2001b, Marston et al. 2002). Thus, the ecological roles and population sizes of other anadromous fishes, both past and present, need to be addressed.

Conclusion

In *A Sand County Almanac*, Aldo Leopold (1949) described the incremental movement of atom X from headwaters to ocean, driven by the forces of gravity and discharge, to its ultimate "prison" in the sea. Understanding the implications and controls of "nutrient spiraling," as this phenomenon has been termed, has driven much of recent stream ecosystem research (e.g., Peterson et al. 2001). Our current understanding of the phenomenon of salmon-derived nutrient input clearly shows that a small but important proportion of those atoms escape their "prison" to return in the bodies of ocean-dwelling organisms, whose behavior drives them back against gravity and stream discharge to penetrate the continent. Quantifying the ecological effects of this phenomenon and translating that understanding into useful conceptual and practical tools to better manage oceanic, freshwater, and terrestrial ecosystems—without reference to the jurisdictional, organizational, and conceptual boundaries that currently inhibit us—remains a challenge for scientists and managers alike.

Acknowledgments

This manuscript benefited greatly from reviews by Lisa Thompson, Tom Quinn, Tom O'Keefe, Wayne Minshall, and Dominic Chaloner. Stacey Poulson was instrumental in creating the figures. Funding was provided by the USDA Forest Service, Aquatic and Land Interactions Program, Pacific Northwest Research Station, Juneau, Alaska.

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Statement of Ownership, Management, and Circulation		13. Publication Title		14. Issue Date for Circulation Data Below	
1. Publication Title BioScience		2. Publication Number 0 0 0 6 - 3 5 6 8		3. Filing Date 20 September '02	
4. Issue Frequency Monthly		5. Number of Issues Published Annually 12		6. Annual Subscription Price \$50.00 (Individual); \$100.00 (Institution); \$24 (Student and Educator); \$40 (Library)	
7. Complete Mailing Address of Known Office of Publication (Not printer) (Street, city, county, state, and ZIP+4)		8. Complete Mailing Address of Headquarters or General Business Office of Publisher (Not printer)			
1444 I St. NW, Suite 200, Washington, DC 20005-1500		Contact Person Herman Marshall Telephone (202) 628-1500			
9. Full Names and Complete Mailing Addresses of Publisher, Editor, and Managing Editor (Do not leave blank)					
Publisher (Name and complete mailing address)		Richard T. O'Grady, 1444 I St. NW, Suite 200, Washington, DC 20005-1500			
Editor (Name and complete mailing address)		Tim Beardsley, 1444 I St. NW, Suite 200, Washington, DC 20005-1500			
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PS Form 3526, October 1999		(See Instructions on Reverse)			
13. Publication Title		14. Issue Date for Circulation Data Below			
BioScience		August 2002			
15. Extent and Nature of Circulation		Average No. Copies Each Issue During Preceding 12 Months		No. Copies of Single Issue Published Nearest to Filing Date	
a. Total Number of Copies (Net press run)		7196		7450	
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f. Total Free Distribution (Sum of 15d (1) and 15e)		437		566	
g. Total Distribution (Sum of 15c and 15f)		6720		6757	
h. Copies not Distributed		476		693	
i. Total (Sum of 15g and h.)		7196		7450	
j. Percent Paid and/or Requested Circulation (15c divided by 15g times 100)		93.5		91.6	
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