

THE YEARLY RETURN OF SALMON from the open Pacific Ocean to coastal waters of Western North America is one of nature's grand displays and recent investigations by researchers in Washington, British Columbia and Alaska indicate that the signature of salmon finds its way into both aquatic and terrestrial ecosystems, as far inland as the Rockies.

The most widespread species associated with these formerly immense schools of salmon are black and grizzly bears, which migrate from alpine and distant habitats to congregate along streams and rivers during the spawning migration. Recent studies show that these predators play a much more significant ecological role in coastal forests than previously recognized.

During an investigation on the foraging behaviour of Queen Charlotte Island black bear, begun in 1992, I found that bears individually captured about 700 largely spawnedout salmon over the six-week spawning period and carried the majority of these into the forest where they could feed relatively undisturbed. At Bag Harbour, where most of the data were collected, eight bears transferred 3,000 salmon into the forest over the one kilometre of stream where salmon spawned. On average, about one-half of each salmon carcass was consumed by the bears and the remnants were scavenged by eagles, marten and flocks of crows, ravens and gulls. A diversity of insects including flies and beetles were found with the carcasses and typically within five days, all carcasses were a seething mass of maggots which consumed all remaining soft tissues, leaving the bone. The cumulative effect of decomposing carcasses combined with the faecal and urine discharge from bears and other animals pro-

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duces a highly odiforous riparian zone.

Expansion of these studies on the Queen Charlottes indicates that transfer of salmon carcasses into riparian zones is widespread throughout the British Columbia coast wherever bears and salmon are common and these nutrients represent a significant part of the nitrogen budget of vegetation and soil invertebrates. The use of stable nitrogen isotopes allows us to identify the relative contribution of salmon to the ecosystem. Researchers have

Our research over the last decade, combined with those of other investigators in the Pacific Northwest, has yielded previously unrecognized linkages between the open ocean and forests. noted that ¹⁵N, the heavy but rare isotope of nitrogen, is more abundant in marine algae than in terrestrial vegetation. Rasmussen at McGill University, and others, have shown that the isotope is further enriched with each successive trophic level.

Salmon, occurring at the 4th trophic level in marine waters, are very enriched in ¹⁵N. Consequently, comparisons of ¹⁵N levels in vegetation beside a salmon stream with control plants nearby without access to salmon provides a direct meas-

ure of the contribution of salmon-derived nitrogen to the plants. Researchers in Alaska and Washington, such as Kline, Bilby and Ben-David, have shown evidence for ¹⁵N enrichment in aquatic and streamside vegetation. My student, Deanna Mathewson, has looked at needles or leaves from 10 riparian plant species, including Western Hemlock, devil's club, false azalea, red huckleberry, salmon berry, buckbean and false lily of the valley from some 20 watersheds throughout the British Columbia Coast that differ in abundance of salmon. These data demonstrate that up to 40 percent of the nitrogen used by the riparian plants is derived from salmon nutrients, with values dependent on the salmon density in the stream, abundance of bears, plant species and distance from the stream.

Another student in my lab, Morgan Hocking, is examining isotope signatures in insects and other invertebrates and has shown major amplification of ¹⁵N at multiple trophic levels, including herbivores, omnivores, carnivores and detritivores. This amplification does not extend from direct consumption of salmon carcasses but rather from indirect food web effects. Dr. Jonathan Moran, another member of our group, has examined nitrogen isotopes in soil at increased distance from the stream at each of six watersheds differing in the numbers of salmon and finds a direct relationship between soil ¹⁵N and salmon density.

That riparian plants or insects are using salmon-derived nutrients does not itself provide evidence that this source of nutrients is required or essential for the plants. One line of evidence that plants directly benefit from salmon nutrients would be evidence for improved growth rate in trees. Nitrogen is usually limiting in coastal forests, as can be readily seen by the positive effect of adding fertilizers. At Bag Harbour, these carcasses contribute up to 120 kg nitrogen per hectare into the forest, comparable to applied fertilization rates by industry in coastal forests.

As a preliminary test of this, I examined yearly growth rings of Western Hemlock at Bag Harbour of 13 trees of similar size from sites differing in carcass density. Average growth rate over the last 50 years was 2.5mm per year within 10m of the stream where carcasses were most abundant and less than 1mm per year where carcasses were not present.

Furthermore, individual trees grow more rapidly following years with high salmon abundance, while control trees nearby without access to salmon show no changes in growth for the equivalent period. These data are at best ambiguous, as multiple factors influence plant growth, including light, moisture and nutrients. I am currently examining yearly growth in Western Hemlock and Sitka Spruce from 80 watersheds throughout the British Columbia coast differing in abundance of salmon and a variety of physical parameters in an effort to partition the influence of salmon from other factors. Some of our study sites are particularly useful as they include comparisons of trees immediately above and below waterfalls that are impassable to salmon.

One of the empirical observations emerging from the Bag Harbour studies was that the amount of salmon transfer into the forest each year varied directly with the yearly numbers of spawning salmon returning to the stream. As such, it seemed plausible to me that yearly differences in this nutrient pulse might be reflected in the ¹⁵N levels in yearly growth rings of the conifers. If so, the rings might retain evidence for past fluctuations in salmon nutrients and potentially allow a reconstruction of movement of salmon into the watershed into past centuries. This has proved, however, logistically challenging due to the difficulty in detecting ¹⁵N in wood. Standard mass spectrometers, the instruments used to measure isotopic ratios, work well with leaves or needles in which the carbon to nitrogen ratio (C:N) is about 40:1. Yet, the C:N ratio in wood is about 1000:1 and as such, the signature of ¹⁵N is masked by the large amount of carbon. Over a three-year period and in collaboration with colleagues at McGill University, wood samples were sent out to four different mass spectrometer laboratories but none could produce a repeatable ¹⁵N signature. In 1998, I sent some wood samples from Bag Harbour to a mass spectrometer researcher from California and he was able to gradually solve technical constraints and measure ¹⁵N on yearly growth rings of Western Hemlock and Sitka Spruce. The excess carbon in the samples remains a constraint and progress is slow. To the present, I





DR. T. E. REIMCHEN Department of Biology, University of Victoria, BC. E-mail will reach him at reimchen@uvic.ca have sent wood samples from 25 trees and the results can be briefly summarized .

Comparisons among watersheds shows that the ¹⁵N levels in the wood of trees adjacent to streams is directly proportional to salmon numbers. The highest values, near 10 parts per thousand, occur in ancient Sitka Spruce at a mid-coast stream near Bella Bella that has the highest salmon spawning density identified in our studies (60,000 salmon /km). Up to 80 percent of the yearly nitrogen budget in some years in these spruce appears to have been derived from salmon nutrients.

Comparisons within watersheds show that the ¹⁵N levels are highest in trees near the stream and decline with increased distance into the forest, concordant with the decline in salmon carcasses and bear activity. Even in small watersheds, vegetation 150 m from the stream still has the signature of salmon. This suggests a much broader riparian zone than the 10-30 m zone suggested in government policy on fish streams. Recent studies by Hilderbrand in Alaska suggest that the salmon signature in vegetation occurs some 800 m into the forest where grizzly bears are common.

Comparisons within trees demonstrate a correlation between ¹⁵N signatures among yearly growth rings and DFO records of salmon escapement over the last 50 years. The peaks in salmon can take from one to three years to show up in the tree rings.

Older or larger trees exhibit higher ¹⁵N levels in growth rings than younger or smaller trees. This could reflect either increased transfer of salmon nutrients to larger trees or increased isotopic fractionation (reduced uptake of ¹⁵N) of young trees when the static nitrogen supply in the soil may exceed the requirements.

The research is ongoing and we have taken cores from 750 trees at 80 watersheds along the coast that will be analyzed for dendrochronological and isotopic data. The results will provide a detailed historical assessment of nutrient cycling in watersheds throughout the coast.

Our research over the last decade, combined with those of other investigators in the Pacific Northwest, has yielded previously unrecognized linkages between the open ocean and forests and these may be important to our understanding of forest ecosystems. The available evidence currently suggests that these linkages occur from the estuaries and small streams that fringe the North Pacific through to the headwaters of the major rivers that penetrate far into the continents. The estimated 80-90 percent reduction in salmon returning to streams over the last 100 years, largely the result of deforestation and overfishing, will have ecosystemlevel consequences for the remaining forests. What these are remain largely unknown but more of these effects will emerge from the ongoing research programs. 🖋

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