SFU

Speaking for the Salmon

Salmon and Nutrients: A seminar on science and policy

A SPECIAL SEMINAR OF THE SPEAKING FOR THE SALMON SERIES

PROCEEDINGS

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Craig Orr, Executive Director, Watershed Watch Salmon Society with assistance from Doug Braun, M.Sc. Candidate, Biological Sciences, Simon Fraser University.

The Speaking for the Salmon series *examines issues impacting the survival of wild salmon in British Columbia. Projects in the series include workshops, think tanks, proceedings and video presentations. For more information, visit our website at: www.sfu.ca/cstudies/science/salmon.htm*

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Introduction

Craig Orr, Executive Director, Watershed Watch Salmon Society

We acknowledge the support of our sponsors, the Gordon and Betty Moore Foundation and the Consortium for Genomic Research on all Salmonids Project for making this project possible. We also thank Doug Braun from Simon Fraser University who helped to organize this workshop, and give special thanks to Daniel Schindler and the panellists for sharing their views.

What follows is an edited transcription of the presentations and discussion.

Objectives

The objectives of this seminar were to examine potential influences of salmon nutrients on their ecosystems and to identify the role of the Wild Salmon Policy in delivering sufficient marine-derived salmon nutrients to freshwater and riparian ecosystems. Every year, spawning Pacific salmon deliver large quantities of nutrients to freshwater and riparian ecosystems. Current research has shown that the influence of these nutrient subsidies on ecosystems is variable, making it difficult to quantify the value of salmon nutrients to their ecosystems. One of the objectives of the Fisheries and Oceans Canada Wild Salmon Policy is to include ecosystem values, such as marine-derived salmon nutrient subsidies, in the management of Pacific salmon; however, DFO recognizes the challenges in translating ecosystem values in management initiatives. This seminar and dialogue examined the current research on salmon nutrient contributions to ecosystems with a focus on using this information to advance the implementation of Strategy 3: Inclusion of Ecosystem Values and Monitoring of the Wild Salmon Policy.

We face a number of co-management challenges in determining how many salmon we want to return to these systems. First, the salmon have to go through the fisheries, whether river or ocean, and then we have to determine how many salmon we want to escape for the perpetuation of stocks and also for the welfare of ecosystems, systems that include eagles, bears and marine mammals that depend on salmon for food.

There are also management challenges such as determining how to recover systems affected by aquaculture, such as in the Broughton Archipelago. Most of the pink salmon that are coming back are returning to one river system, the Glendale. There was a crash of pink salmon in 2002—when we expected a return of 3.6 million fish, there were only 147,000. That is a 97% decline in expected returns and the majority of those fish returned to the Glendale. It was worse in 2008 when the return to Glendale was 15,000 fish from a brood of 187,000. The challenge is to determine how many fish should return to these systems and what should the distribution of those fish be? In addition to a Coordinated Area Management Plan being developed by Marine Harvest Canada, we are also in the process of developing a monitoring and evaluation plan for the successes of this plan and determining how we might predict the pressures on pink salmon.

The question for the Broughton in terms of the Wild Salmon Policy is: How are these fish distributed in terms of genetic diversity and capacity, as well as numbers for the ecosystem?

Introduction of the Keynote speaker

Doug Braun, M.Sc. Candidate, Biological Sciences, Simon Fraser University

Daniel started his academic career at the University of British Columbia and then moved to the University of Wisconsin where he acquired both his MSc and PhD. Supervised by Dr. James Kitchell, his PhD dissertation looked at the role of fishes in habitat coupling in lakes. Daniel then became an Assistant Professor in the school of Aquatic and Fishery Sciences at the University of Washington where he currently holds the H. Mason Keeler Chair in Sport Fisheries Management. He has published over 70 peer reviewed articles. He is also an Associate Editor for *Ecology* and *Ecological Monographs* and he serves as a trustee for the Nature Conservatory in Washington.

Daniel's approach to research is both experimental and theoretical, coupling field ecology with simulation and statistical modeling. His current research focuses on understanding the causes and consequences of dynamics in aquatic ecosystems, more specifically, how species interactions drive the transfers and transformations of energy and matter in ecosystems.

Daniel often steps out of the traditional academic role and applies his research to management and conservation. He conducts much of his recent research in Alaska as part of the Alaskan Salmon Program. Through this program and collaboration with the Alaskan Department of Fish and Game, his research findings contribute to the management of salmon fisheries. Daniel's presentation will explain his research on salmon-derived nutrients and the dynamics of coastal ecosystems, as well as give insights into how this body of research can help inform management and conservation of Pacific salmon in British Columbia.

Salmon-derived nutrients and the dynamics of coastal ecosystems: how good is the story?
Daniel Schindler, Professor, Aquatic and Fisheries Science, University of Washington

I share my perspective on one of the best stories in natural resources and aquatic ecosystem ecology; it is the story about the importance of salmon as vectors of nutrients between the ocean and fresh waters. The story begins when juvenile salmon are hatched in gravel somewhere in a stream. They eventually migrate to the ocean, spend a couple of years avoiding predators and maturing, and then make what is often a long, arduous migration back to their spawning grounds where they dig their redds, lay their eggs and propagate the next generation. As a final sacrifice in their challenging life cycle, they die and fertilize the nursery habitat with the nutrients in their bodies.

This story captures the attention of many, whether they are scientists, the public, or managers. I would argue that the story has reached almost biblical proportions in terms of how well it has become embraced and the vigor with which it is told. However, I would also argue that the facts are rarely checked. The story keeps being perpetuated and I think it is time that scientists who study salmon make a new assessment of how important these effects are and where the effects need to be incorporated into management. I will provide an overview, focused on my research from Bristol Bay, Alaska, where salmon populations are doing very well. I will also highlight some of the things that we are learning about the role of marine-derived nutrients for salmon productivity and for the productivity of their ecosystems, and in some cases, animals and plants that we are interested in for other reasons.

In the last 20 years, there has been increasing research effort to understand how important marine derived nutrient shunts are. One of the motivations for this has been the fact that salmon populations in the lower 48 are severely depressed, with most stocks being around 5-10 percent of best estimates of historical density. There is interest, often motivated by the Endangered Species Act, to recover these stocks. In places like Alaska, the populations are close to pristine condition in terms of total fish production, but of course the fisheries are operating and removing 50-80 percent of the fish before they return to fresh water to spawn. Even in places where salmon are abundant, much of the marine derived nutrient shunt is intercepted and the resulting effects of this loss of nutrients are not well understood for the recipient freshwater and riparian ecosystems.

Here is an example of "the story". A key paragraph in "Salmon, Wildlife and Wine: Marine derived nutrients in human dominated ecosystems of central California", published recently in a peer reviewed, reputable journal (Ecol Appl 2006-06-01, 16(3):999-1009), the author notes:

> *The salmon subsidy results in an increase in the abundance or growth rate of aquatic invertebrates and fish and riparian tree production. Salmon derived nutrients are also part of a positive feedback loop that benefits salmon populations. These nutrients cause aquatic and terrestrial insect populations to increase resulting in faster growth, [etc ...]. The complexity of the stream habitat for both juvenile and spawning salmon also increases when large salmon fertilized trees fall into the water.*

The author, like many other scientists, concludes:

> *In light of this overwhelming evidence of salmon importance over many scales of ecological function there have been calls for managers to take into account the role of salmon nutrients in aquatic and terrestrial systems.*

Managers are facing "the story" and asked to do something about it. Some of the managers ask in return "Show me where it is important and tell me what I need to do about it?" That is where I think scientists have failed. We have failed to point out exactly where marine-derived nutrients mean something for the dynamics of the resources that these managers are managing. We have also failed to give any advice on how management should change to embrace these things.

This presentation will focus on the following:

- Marine derived nutrient effects on sockeye lakes
- Salmon effects in stream ecosystems
- Salmon effects on consumers
- Salmon effects on riparian productivity.

Marine derived nutrient effects on sockeye lakes
When I worked in BC for the Salmon Enhancement Program, one of the things we were interested in was how nutrient loads to lakes affect the productivity of those lakes and their ability to support sockeye. I am going to provide an evaluation of this from lakes in Alaska, and will address the cumulative effects of salmon in streams.

Sockeye are often dominant and can achieve very high densities in runs returning to coastal or interior lakes. The fish are intercepted first by a fishery, and then spawn in streams or on lake beaches. They spend the first year or two of their lives in the recipient lakes where the nutrients released by the adult population have fertilized and enhanced the capacity to support juvenile salmon. By intercepting marine derived nutrients through the fishery, smaller and smaller salmon in the system are produced because of the reduction of the overall nutrient load to the system.

Despite the large amount of effort and money in Alaska and British Columbia and other places put into fertilizing lakes, no one has evaluated what the effect of the marine derived nutrients is on salmon productivity. There have been good examples of evaluations of the question: When we fertilize lakes, how does fertilization translate into changes in salmon production? But the appropriate experiments that allow both higher densities of fish and their related nutrient loads have not been done.

A few of us have used a paleolimnological approach to take sediment cores out of lakes that have dense salmon runs to reconstruct both historical salmon densities and identify some indicators of how productive the lake was, from the perspective of primary production, to assess how the lake production is linked to the productivity of salmon coming from that system. The lake is a sedimentation basin and at the bottom of the lake is a large pile of sediments that are layered down in successive strata. A sediment core can be extracted out of those and the history of that lake can be reconstructed by examining changes in the sedimentary isotopic signature, nutrient source indicators, and algal abundance. It turns out that salmon come in from the ocean after feeding at a relatively high trophic position and have an enriched nitrogen isotope signature that can be traced quantitatively into lake sediments. Figure 1 shows a core spanning of about 250-300 years for a lake in Bristol Bay, Alaska.

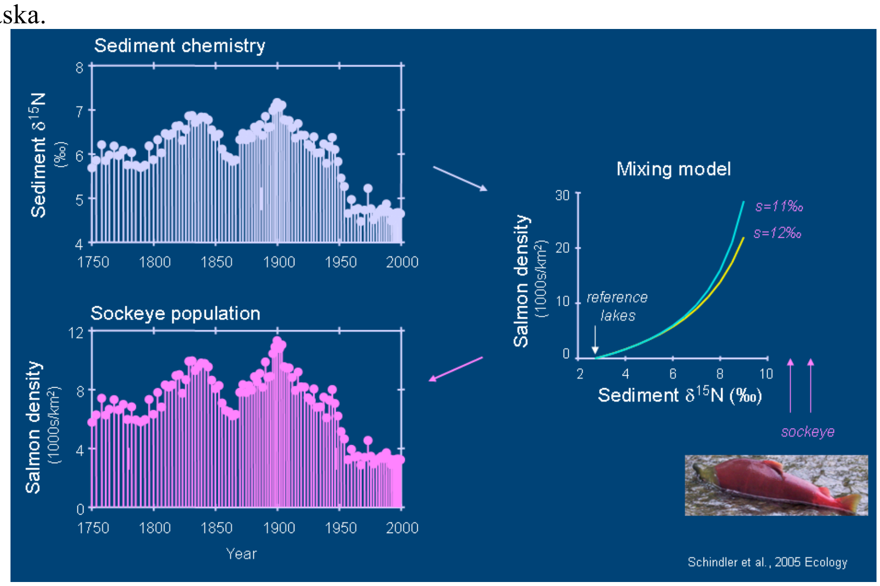

Figure 1. Reconstructing historical sockeye population dynamics from lake sediments (Schindler *et al*, 2005 Ecology).

The Nitrogen 15 signature varies up and down between 6 and 7 percent until about 1900 when the first canneries were developed there, after which it declines to a significantly depleted level compared to the pre-historical levels. At a reference site, not included in the figure, there is a small wobble, but it is usually much flatter and less enriched with the heavy N15. We can model this and reconstruct the salmon population dynamics. Not surprisingly, what many of these cores show is at the time of commercial fishery development, a large number of fish were intercepted and their nutrients no longer showed up in the lake sediments.

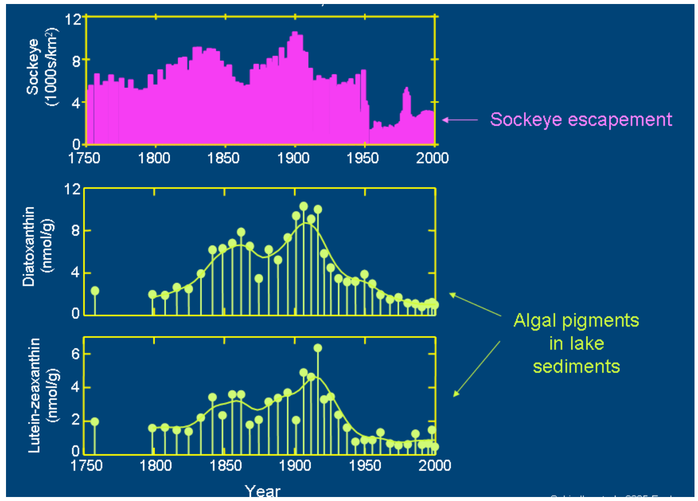

Figure 2. Effects of sockeye population on phytoplankton production in lakes (Lake Nerka, SW Alaska) (Schindler *et al*, 2005 Ecology).

That does not answer the question about whether or not the lake was more productive from either the perspective of algae or salmon. The first step towards answering this question is encompassed in the work I did with Peter Leavitt at the University of Regina, who studies algal pigments. Many pigments decompose, but some of them are relatively stable and when they are deposited in sediments you can reconstruct the concentrations and estimate how productive the lake was relative to its historical conditions. The top panel in Figure 2 is a reconstruction of how many salmon returned to Lake Nerka in southwest Alaska. It wobbles around and peaks around 1900 and then declines to levels that are about one third of what it was at a time when the fisheries developed.

The figure shows the responses of the lake algae which also peak around 1900 when the concentrations decline to about one third to one quarter of these historical levels. These results were reassuring. When two thirds of the nutrients of a system were intercepted, the overall primary productivity of the system was reduced by roughly one third or one quarter of what it was. If we do a nutrient budget, salmon are one of the key sources of nutrients in a system. If that source of nutrients is removed, the lake is no longer as productive.

Figure 3 shows the correlation for the last 300 years between the enrichment in the sediments and the concentration of pigments produced by diatoms in several lake systems. The plots in the top four panels show data for lakes that have relatively high sockeye densities. Surprisingly, you see strong and positive relationships between these two variables; as salmon density increases the amount of algae produced also increases. The bottom two plots represent two reference systems, where the direction of the correlation is opposite and this has to do with some of the biogeochemistry of the system.

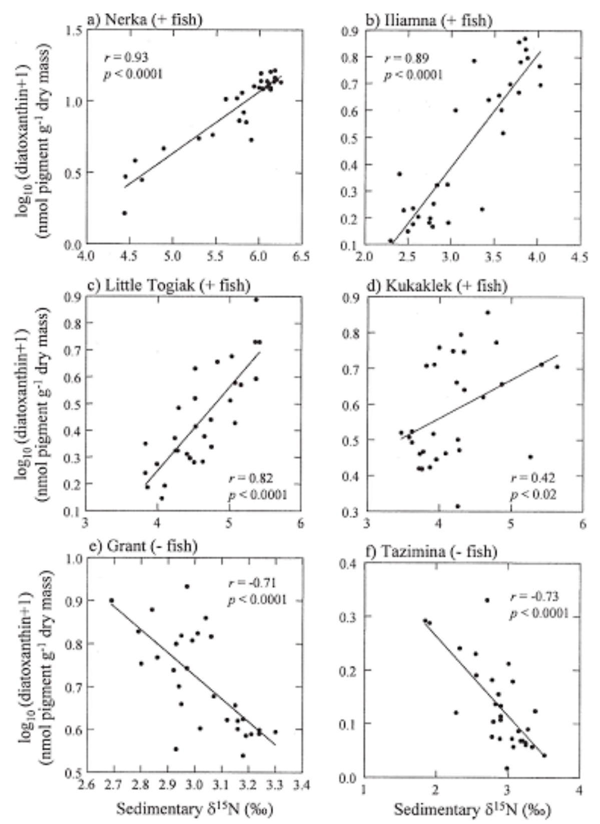

Figure 3. Correlation between diatom production and sediment δ^{15}N (~escapement) (1700- 2000, Bristol Bay, Alaska) (Brock *et al*., 2007).

We can take the strength of these correlations, run them for the last 100 years, and ask "How responsive were these lakes to interception of the nutrients?" In Figure 4, we have plotted the correlation coefficient between algal production and salmon density as a function of the proportion of the nitrogen budget of these systems that is derived from salmon. As the proportion in the system increases, there are stronger and stronger correlations between the influx of salmon nutrients and the corresponding lake algal productivity. Also, at sites where the marine derived nutrient source is a small component of the nitrogen budget, these two variables are much more independent. These data convinced us that primary productivity of these systems, especially during the last 100-300 years, was intimately dependent on the marine derived nutrient subsidies to the lakes, and that because of commercial fisheries, the lakes were less productive in terms of algae than they were pre-historically. However, we must remember that we are trying to manage salmon. People managing fish do not necessarily care about algae unless the algae have something to do with how many fish are produced.

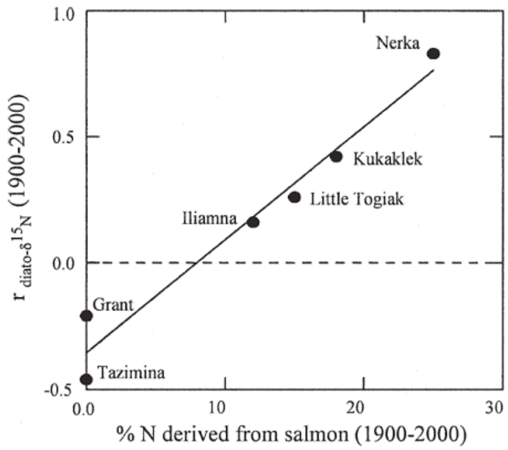

Figure 4. Correlations between diatom production and sediment $\delta^{15}N$ (~escapement) (1900 – 2000, Bristol Bay, Alaska) (Brock *et al*, 2007 L & O).

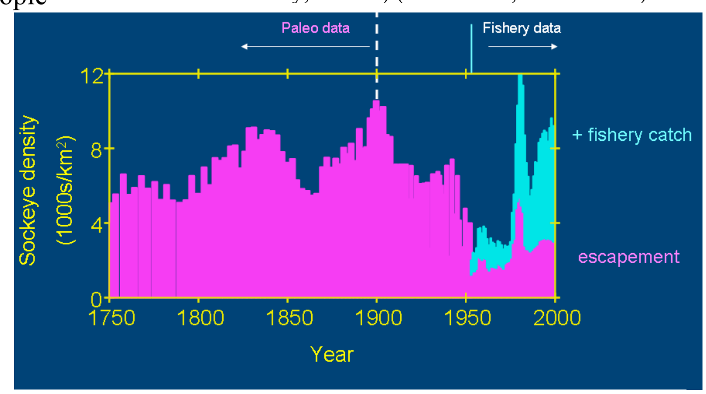

Figure 5. Historical sockeye population dynamics (Lake Nerka, Bristol Bay, Alaska 1750 – 2000) (Schindler *et al*. Ecology 2005).

What we are really asking is: How do these changes to the nutrient status of a lake affect the dynamics of the salmon populations themselves? To answer this question we added the fishery catches over the last 50 years to the estimates of escapement to establish the total run size over the last 50 years (Figure 5). Note that escapement plus catch for the last 50 years is quite variable, but since about 1977, the time period when the North Pacific shifted to a more productive phase, the total fish produced by this lake was about 10-15 percent higher than at any time in the past. In fact, the peak production estimates were higher than they were for a short period around 1900. From these data, and for this single lake, we argued that interception of the marine derived nutrients reduced the primary productivity of the lake, but had no effect on how many salmon were produced by the lake.

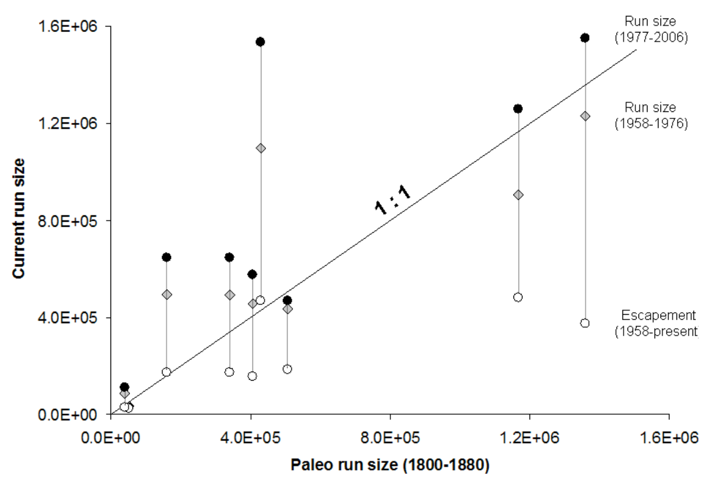

Figure 6. Western Alaska sockeye salmon production; prehistoric versus today (Schindler and Leavitt unpublished).

We expanded this analysis and Figure 6 shows results from nine other lakes where we compared the average density between 1800 and 1900 (which is before the commercial fishery developed) to the last 40 or 50 years that has enumerated escapement plus enumerated catch. The X axis represents the estimates based on paleolimnology of how many fish there were between 1800 and 1880—some of these fisheries developed in the late 1800s. The Y axis represents the current run size. The diagonal is the 1:1 line and the open circles are the escapement estimates. Not surprisingly, they fall well below the 1:1 line—we are catching fish and intercepting them before they come back and their nutrients are archived in the sediments. The slope of this line is about 35% of the 1:1 line, which actually corresponds very well to the exploitation rate (65%) of these systems.

The grey diamonds show the run size from 1958-1976, when the PDO was in a cool, unproductive phase. The dark points are observed production from 1977 to 2006. In all the lakes, but one, there is substantially more production in these systems now than there was in the 1800s. This is true even for the periods of low productivity scattered around the 1:1 line, depending on what system you pick—some are below and some are above. In only one case is there a lake where the current run size is near to or just below the 1:1 line. This suggests to us that even though two thirds to three quarters of the nutrients that would normally be brought back by salmon to these nursery lakes were intercepted by the fishery, the lakes are at least as productive as they were before the advent of commercial fisheries. This does not mesh well with "the story". The story is that if we remove the marine derived nutrients then the whole thing falls apart. Why is there a discrepancy?

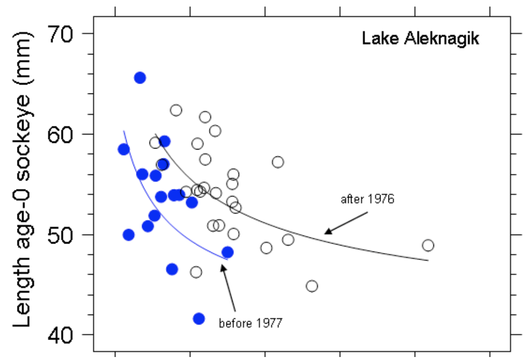

Figure 7. Density dependent juvenile sockeye growth (length on Sept 1, 1960-2007) (Schindler unpublished).

One of the reasons for this is that the scientists who have worked on the marine derived nutrient issue have not been reading fisheries literature, and vice versa. Commonly in fisheries data, you see density dependent growth and survival of juveniles, and in many cases density dependent spawning success of adults. The program in Bristol Bay has been running since the late 1940s. We have a fifth data set, started in 1960, of the size of juvenile sockeye salmon at the end of their first year growth as a function of how many parents produced them (Figure 7). There is a strong negative relationship, which can be split out into two different regimes. The closed circles represent the cold regime before 1977 and the open circles represent the period after the PDO regime shift when the climate warmed up and the lakes became ice-free for longer periods of time and the waters were warmer. The point is that the fish grow best at low escapement densities. The reason for this is that if there is a big escapement, then there are many competing mouths to feed and they do not grow as much. Climate on top of density-dependence has had an effect such that during the last 30 years these juveniles grew substantially better than during the cold phase. The point here is that density dependence is key in this system. As the number of fish in this system is increased, competition is increased and this effectively decouples the nutrient subsidy to primary production from the actual growth and survival dynamics of juvenile fish. Kim Hyatt was one of the leading scientists of the Salmon Enhancement Program in British Columbia, in the fertilization program of DFO. Lake fertilization studies were not necessarily wrong. What the lake fertilization studies did was to move lakes from the curve upwards such that juvenile fish grew at faster rates, for a given escapement. At a constant density, or some constant range of densities, fertilization in some cases did enhance the overall capacity of the system to support juvenile fish growth. In Figure 7, the enhancement was due to temperature. In some of the cases from BC and Alaska enhancement is attributed to fertilization by non-salmon nutrient sources.

One of my first messages is that we need to collaborate. Fisheries science has a rich body of theory, data and statistical techniques that the marine derived nutrient scientists have not yet accessed. Fisheries scientists need to start talking to marine derived nutrient scientists, myself included. An example of this is described in the following scenario. One of the hallmarks of population dynamics is the stock recruit function that involves taking the stock size, in terms of numbers of fish that spawn, and looking at how many recruits they produce. The question is: What does this function look like if you consider the amount of marine derived nutrients in the system? The "story" envisions a model indicating that as the amount of fish in the system increases, the carrying capacity of system increases. There is talk about a "positive feedback" and we saw that in the excerpt that I shared earlier.

The problem with this is that it does not make quantitative sense. You add positive feedback to the carrying capacity and suddenly the world is swimming in fish. There is no boundary on the system. It just spins out of control and you have an infinite number of salmon in the world. We know that this is not a possibility. What is another possibility?

Another possibility is depensation, such that marine derived nutrient feedback is most important at low salmon densities, where the last few juveniles left in the stream are starving to death because there are not enough marine derived nutrients coming back to feed them or their ecosystems. However, if that were the case, then we would not see negative density dependence and juvenile growth. In fact, it is usually the case that juvenile salmon grow best at extremely low escapement densities.

To throw another measure into the mix, consider the Ricker curve. Bill Ricker cut his teeth on sockeye and the Ricker stock recruit function is one of the most used functions in salmon management. One of the things it does is bend over such that with a high stock size, according to a Ricker model, you can actually get reduced production by the next generation. Fishermen in Alaska love using this model and they have a term that they call "over escapement", which is a good excuse to catch more fish. Their point is simply, that under conditions where you do not catch enough fish you swamp the spawning grounds with juveniles and adult salmon and they compete with each other more than they would at "optimum" numbers, resulting in reduced production.

Fisheries science has a very formal set of theories and models to assess how populations respond to changes in their densities. I would argue that marine derived nutrient science has done little to embrace this. This needs to change because in the case of sockeye from the lakes in Alaska, it looks like the best model is probably one of the saturating functions. What we see is there are no enhanced returns from exceptionally high densities. As a test, if you have someone walk into your office and start telling you the story about marine derived nutrients, ask them to sketch out what the stock recruit function should look like to enable the processes that they think are important in the system. I am guessing that they will give you a blank stare. This is an exercise we should all do.

Salmon effects in stream ecosystems

In many ways there are parallels in stream ecosystems to the lake research. However, many recreation activities are focused on streams, so I think there are some other important points to consider, especially since the communities in these streams are benthic and most of the lake communities that sockeye rely on are pelagic. There is the traditional model embraced by the "story"—where the salmon return to spawn, their last sacrifice is giving up their nutrients to their babies, these nutrients funnel up through algae and create more algae, boost invertebrate production and therefore boost fish production. The idea is that as the numbers of salmon in the system increase, primary production in the system is increased and implicitly the respiration in the system is also increased.

Let's think about what salmon do when they get back to streams, in this case, sockeye. Not only do they die and leave their nutrients for their babies, but also in this case the females clean the place up first. The males, of course, are watching while the females actively dig their redds. In places that have high spawning densities, the whole stream can be roto-tilled several times over in the course of a spawning season. What this does is mobilize nutrients.

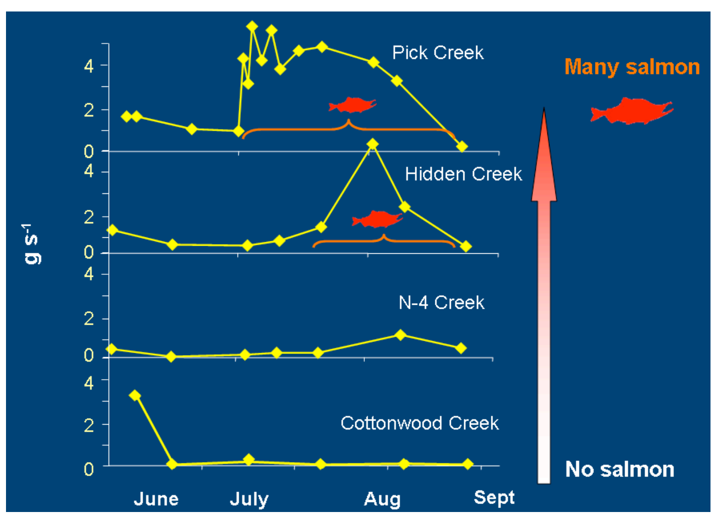

Figure 8. Export of fine sediment (J.W Moore 2008).

Figure 8 shows types of streams, ranging from those that have a lot of salmon to those that have essentially no salmon. This is a measure of the amount of particles that show up in a two litre sample of water over the course of a season. In the non-salmon streams most of the sediment transport is in the spring during the high flow rates. In the salmon system a large amount of sediment is exported during the spawning season. The reason is that the salmon are digging it up and the nutrients are getting moved down stream, in this case eventually settling out in a lake basin. This digging activity is in fact cleaning up the stream and transporting nutrients in the process.

My former graduate student, Jon Moore, calculated how much export sediment is produced by salmon and it is the integral under all these curves. In two sites of relatively high salmon densities, several grams per second of material are moved out of the stream, material that would otherwise accumulate in the absence of salmon. If this is translated into the nutrients in that sediment then you can calculate the amount of nutrients that are exported via this bioturbation by salmon. This is one stream with a relatively high salmon density with about 8,000 sockeye per 2km of stream. This sounds large for many BC systems, but it is a moderate level for most Alaska systems; however, two thirds of those have been caught already. Salmon import about 16 gm^{-2} of nitrogen in their carcasses, but it turns out that their bioturbation does not have much effect on the nitrogen flux because most nitrogen in streams is not particulate—it is in dissolved form and is getting flushed out.

Let's look at phosphorus. The amount of phosphorus imported by salmon migrations is roughly equivalent to the amount that they export due to their bioturbation activities. Both the lakes and the streams in this case are phosphorus limited systems. We have performed bioassays of this phosphorous and have found that it is highly reactive. The point is that salmon are causing inputs to the system and they are exporting it by digging it up and moving it downstream. Again this is the sort of thing that has not been included in "the story".

Figure 9. Male salmon with female digging her redd (J.W. Moore 2008).

What effects does this bioturbation have on the benthic communities?
I will focus primarily on algae and a little bit on benthic insects. If you think about the bottom of these streams being roto-tilled and turned over and buried, then not surprisingly, there are severe negative consequences for the community. Figure 9 shows a pair of salmon—note where the female has dug her redd. What looks black is an algal pigment but remember this is a shallow stream. All the algal biomass has been scoured out and moved downstream and this can be quantified. In one of our key study streams, shown in Figure 10, there is an algal biomass for most of the open water season. It peaks in spring, dips in mid-summer and then increases a bit in the early fall. We can do this for several streams in the area that have a lot of salmon in them.

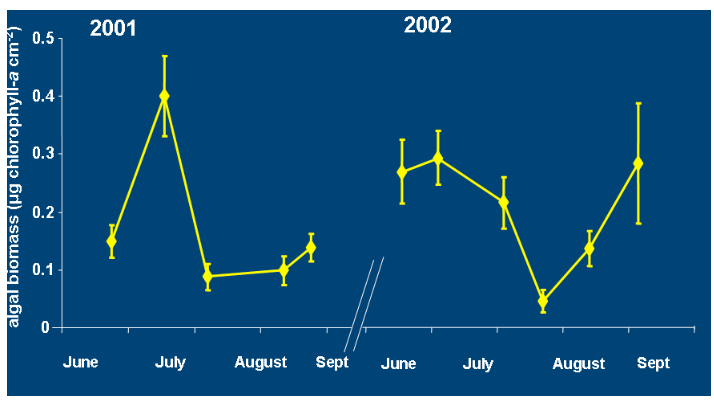

Figure 10. Algal dynamics (Mean ± SE) (J.W Moore 2008).

If salmon density is overlaid on top of that, then not surprisingly, the two time series are negatively correlated (Figure 11). When salmon are absent from the stream, the stream is more productive—at least from the perspective of accumulating algal biomass. The salmon move in, the females dig the redds and algae biomass either gets buried or scoured out of the system.

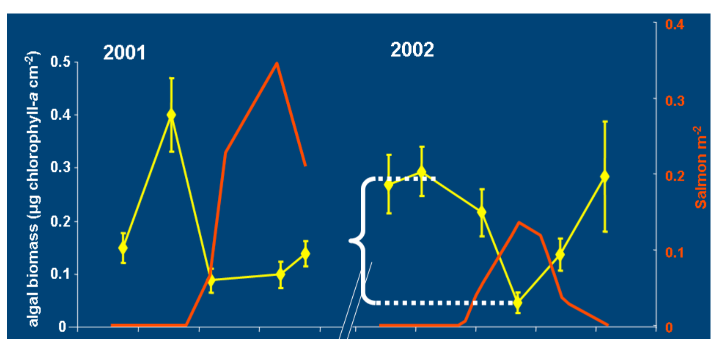

Figure 11. Quantifying impacts of salmon on stream algae—Pick Creek (J.W. Moore 2008).

I will show you examples of where we have quantified this difference between the peak density in spring and how low the salmon drive it over the course of the spawning season. I am also going to stratify this by the substrate size. One of the things that becomes key in terms of understanding the effects of salmon in streams is the size of the substrate. If the substrate is composed of large rocks, that tells you something about the hydrologic energy of the stream and there are probably not a lot of salmon there to start with. Sites that have high salmon densities are usually lower energy streams. They have numerous golf ball sized gravel and low hydrological energy. Those are the systems that have high salmon densities and also a high potential for the algal scouring effect.

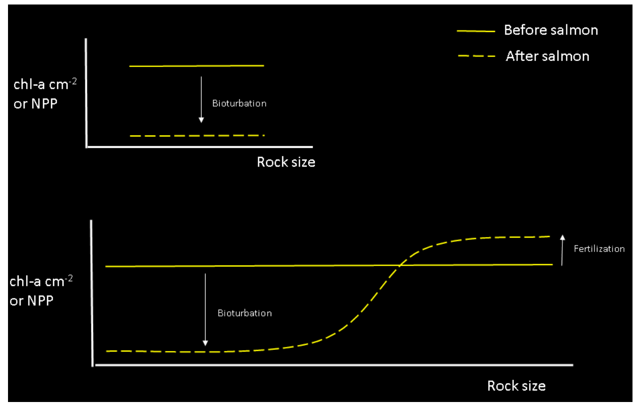

Figure 12. Streams along a gradient of salmon densities and geomorphology (Holtgrieve unpublished).

We wanted to quantify the impact of the size of the substrate on algal composition. Our hypothesis was: If chlorophyll is high before salmon arrive, salmon get there and through bioturbation reduce the steady state concentration of chlorophyll. Then, as the rock size distribution is broadened, bioturbation will knock out chlorophyll densities in cobble size that is small enough to be turned over by salmon and we should see some fertilization effects on big rocks that salmon cannot turn over. Figure 12 shows data from 12 or 15 streams along a gradient of salmon densities and a gradient of geomorphology. Note the class of rocks that are left in the 65 mm median diameter. There is a strong relationship between salmon density and the direction and magnitude of chlorophyll changes before and after salmon. Above 0.2 salmon per m^2 in a stream the algae were scoured and there is much less algae in mid-summer than there is in the absence of salmon.

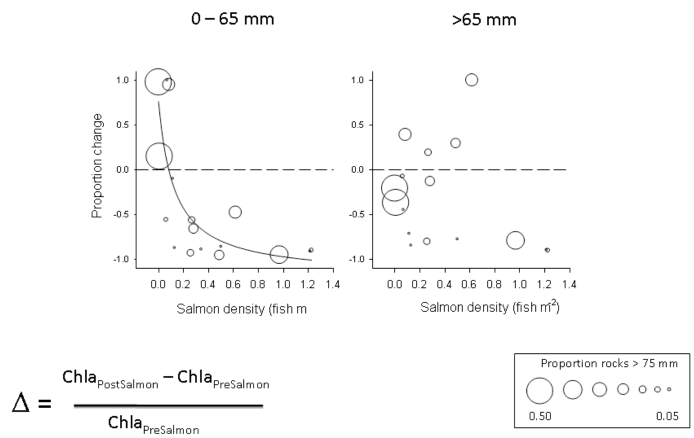

Figure 13. Gravel size effect on algal response to salmon spawning (Holtgrieve *et al*. unpublished).

With bigger rocks, there is a much more complicated relationship. In the example shown in Figure 13, the size of the bubble shows what proportion of the streambed is comprised of rocks >75 mm. If rocks are >75mm, the bed structure becomes much more difficult for the salmon to dig up. There is one outlier in the figure. In this case, even big rocks are excavated and buried by salmon. If more of the stream is characterized by larger gravel sizes, then we can see a fertilization effect, because the salmon are much less effective at roto-tilling the gravel. There does appear to be a geomorphic context for whether salmon reduce or increase algae on rocks. However, we scaled these up to the response of the total system to total system chlorophyll and found that the big cloud of points, nearly all of them, are below zero—some are close to zero. In 2 out of 15 cases there was more algae after salmon arrived in the system. The question is: Are these sites that just do not have enough marine derived nutrients in them to make a difference?

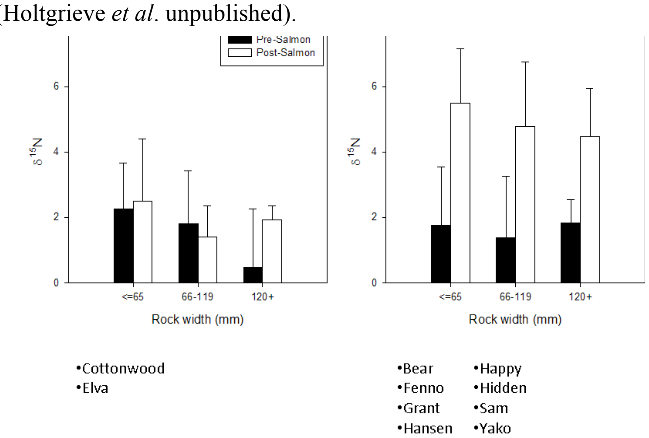

Figure 14. Marine derived nitrogen in stream periphyton (Holtgrieve *et al*. unpublished).

Figure 14 compares the N 15 stable isotope characteristics of algae on rocks. These are two reference streams pre-salmon and post-salmon. There is not much change seasonally before and after salmon on any different rock size. We compare that to salmon streams. Before salmon arrive, the isotope signature on rocks is similar to the reference site, while after salmon arrive the isotope signature is increased. The marine derived nutrients are making it into the algae but there is not much algae there. The fertilizer is there, capable of fertilizing the algae in the system, but the salmon are not just giving up their nutrients. They are also digging up the stream beds and doing their spawning activities and this reduces the algal growth in the system. As a result, most of the nutrients flush out of the stream and down to the lake or estuary.

A recent paper described some possibilities for interactions of land use and the role of salmon in streams. If you account for the substrate size in streams and how the timber harvest may affect the bed morphology of streams for southeast Alaska, the observation is that in large and/or heavily logged areas there is greater transport of small particles, and gravels to streams. As a result, it is easier for salmon to dig them up not resulting in the reduction in the algal concentration. In the absence of the forestry process, there is larger cobble in the systems. The suggestion is that in the absence of forestry more streams are capable of showing a positive response to salmon nutrients. It is a hypothesis and we will see how it holds up. I think it is a good conceptual argument for moving forward to think about some of the multiple stressors on these streams.

That is what algae do in our systems when there is no forestry. These are not exceptionally high salmon densities for Alaska and despite that we are seeing generally negative effects of salmon on algal biomass.

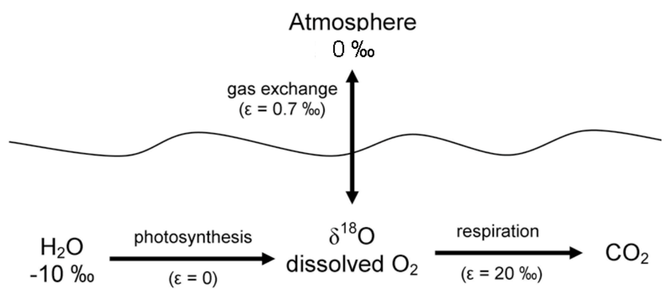

Figure 15. Measuring ecosystem metabolism with O_2 and $\delta^{18}O$-O_2 (Holtgrieve *et al.* unpublished).

What is the response of the overall metabolism of the ecosystem?

We are addressing this question through a study of oxygen dynamics of the system, both from the concentration of oxygen and with stable isotopes of oxygen. Some of our data suggest once again that the conventional model is not supported. Figure 15 shows the tracings of the oxygen concentrations of a stream over the course of a season.

The zigzag pattern reflects the daily pulsing of day/night cycles. By mid-summer this dips down and in fact the stream is significantly below what you would except from atmospheric equilibrium.

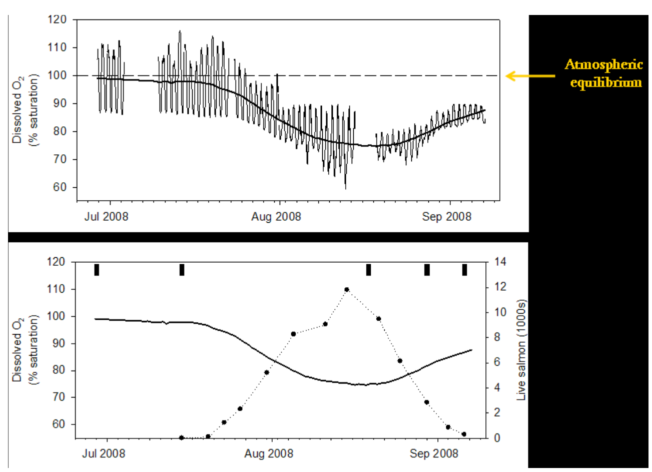

Figure 16. Atmospheric equilibrium curve—Pick Creek (Holtgrieve *et al.* unpublished).

Figure 16 shows the atmospheric equilibrium curve. Note that it corresponds to when salmon are present in the system. We conducted a number of detailed studies with the isotopes during these time periods. They are a very good integrated measure of how productive the system is. In Figure 17 the triangles represent the oxygen concentration around two diurnal cycles, and the circles represent the Oxygen 18 isotope swings.

These two things allow us to estimate respiration and production in the system and changing gasses. Before salmon arrive there is a lot of productivity and daily swings in the system. Once salmon arrive, that disappears. We get rich isotopes and depressed oxygen concentrations, and in fact the concentrations are down to around 70 percent of saturation.

We can do the math as described in Figure 18, which is taken from the work of Gordon Holtgrieve. It accounts for both the isotope mass balance and oxygen mass balance.

Estimates of production and respiration before salmon production are about 180 CI. This is reduced after salmon by about 1.5 times, to 70 $mgmO_2^{m-2h-1}$. Respiration goes from 180 CI to ten times that value.

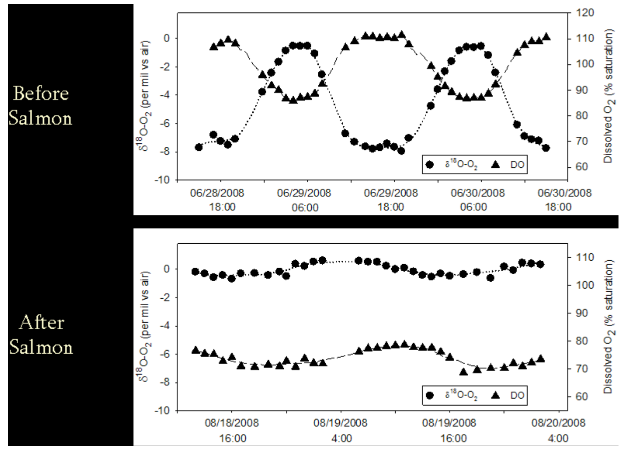

Figure 17. Dissolved oxygen concentration & oxygen stable isotope ratios (Holtgrieve *et al*. unpublished).

If we think about the production to respiration ratio, it is about unity before salmon arrive, as you might expect for a relatively productive system. After salmon arrive, this becomes a very strong oxygen-consuming system and the P:R ratio is less than 5 percent.

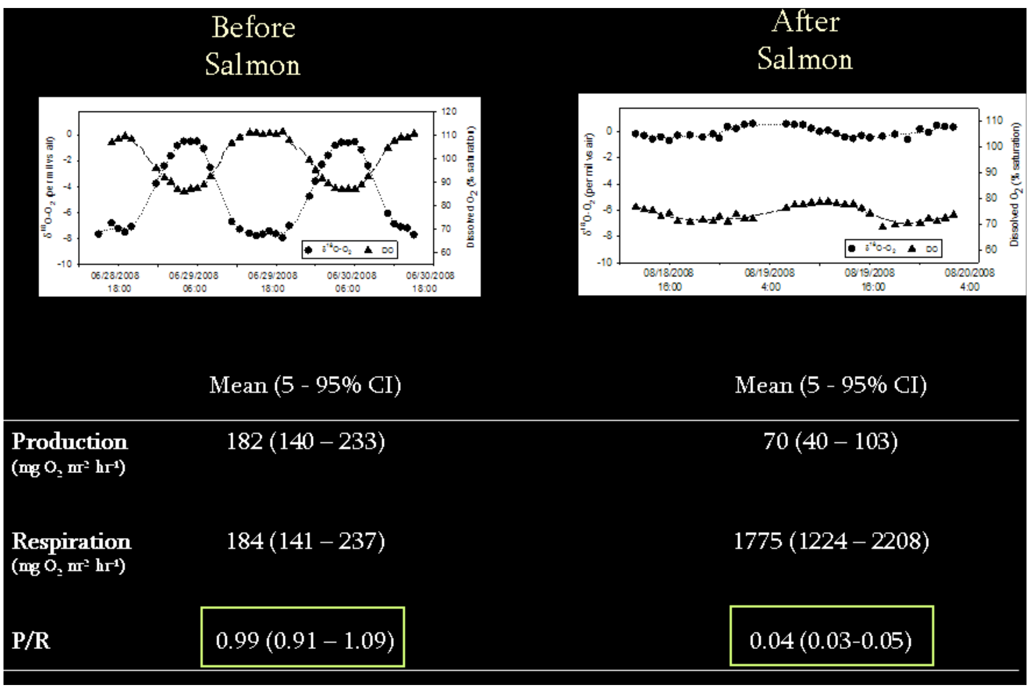

Figure 18. Isotope mass and oxygen mass balance (Holtgrieve *et al*. unpublished).

This does not support the traditional model of what salmon do to ecosystems. Certainly, salmon are contributing nutrients into the system, but the nutrients are not propagated up through the algae. We suggest an alternative model for how that ecosystem responds—one that we are calling an integrated metabolism model that involves an heterotrophic link (Figure 19).

Salmon are both rotting and consuming oxygen, but they are also stirring up the sediments. If we do a carbon budget on the system, we find that

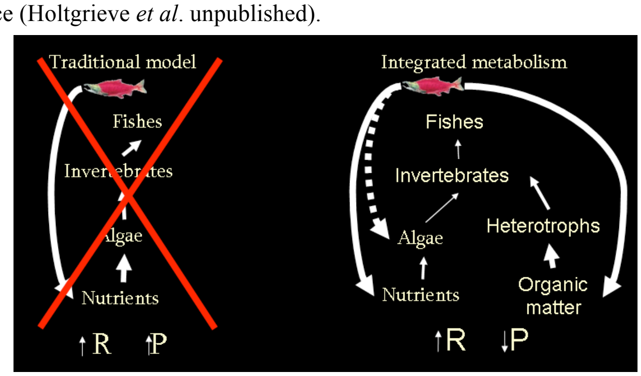

Figure 19. Traditional model compared with the integrated metabolism model (Holtgrieve unpublished).

most of the increase in respiration is due to bioturbation activities that mobilize sediments and much less is due to the decomposition of salmon carcasses themselves.

In this case salmon are taking systems that are oxygen producing or near equilibrium to ones that are strongly heterotrophic. If the densities are even higher, or there are substantially warmer temperatures, there may actually be oxygen deficits large enough to kill fish. This is an argument the fishermen often make. Another argument for this is the over-escapement phenomena, and the oxygen dynamic suggests that this may be partially right.

Salmon effects on consumers

What are insects doing in these sites?

Certainly there are insects such as the caddis flies that do very well and scavenge directly off salmon carcasses—especially ones that are freshly killed by bears. We are finding the same thing with insects as with algae. Insects are getting scoured and buried and their densities decline as salmon move into systems. There are a couple of other papers, including this one that concludes:

> *…this study suggests that the often published positive relationship between marine derived nutrients and stream insect abundance may only exist for certain taxa, primarily midges.*

This frequently published relationship is often from little microcosms where researchers take gravel from a stream, put it in an eaves trough and add pieces of chopped up pink salmon. In doing so, the system is fertilized, and there are more nutrients, more algae, and more bugs. However, if the engineering effects of salmon are included, that is not what we find. One thing that is not yet published but especially interesting, is thinking about how bioturbation may affect the community. Think about your typical aquatic bug. It is flying around as an adult in the mid-summer, and it is laying eggs, most of which are going to over-winter, mature through various nymphal stages during the summer and then emerge. When salmon arrive, late nymphal stages are in a lot of trouble and what we suggest happens is that one way to avoid this and to still be successful as a stonefly or a mayfly is to emerge earlier in the summer.

Jon Moore is doing this work and has found that in systems without a lot of salmon bioturbation, there is relatively constant but sustained insect emergence over the course of the whole season.

Figure 20 shows a site with high salmon density.

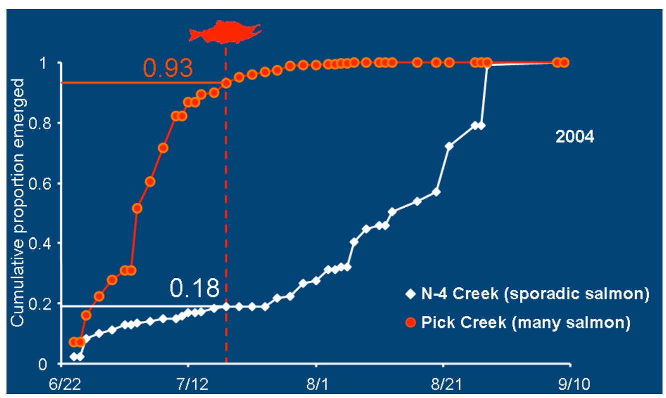

Figure 20. Insects emerge prior to salmon spawning in creeks with high densities of salmon, mean of 5 emergence traps set for 48 hr., all mayflies—predominantly *Aetis* and *Bicaudatus and Cinymula* spp (J. Moore *et al.* unpublished).

It is the same temperature regime and these are similar nutrients. What you find is by the time salmon arrive in the middle of July, 90 percent of the bugs in that stream have emerged and it is void of insects. This suggests that there is a local adaptation in the insect populations to avoid being in the stream while the salmon are there. If you accumulate that over the course of a season, the system without salmon is actually more productive than the system with salmon even though there are more nutrients in the system with salmon. This, we think, is due to the bioturbation effects of the salmon digging.

When we talk about streams, in addition to thinking about the nutrients, we need to think carefully about these engineering effects due to the digging activities of salmon. They affect sediment export and nutrient export, reduce algal abundance, and change the metabolism of the system so that it tends more towards an oxygen consuming system than a producing system. This activity also reduces insect production and changes insect phenology. The geomorphic context for all of these things has yet to be worked out, but I think this is an area of critical study.

How do consumers benefit directly from salmon? This is where the story gets really good since there are several hundred species that eat salmon tissue. Fish eat salmon. Scavenging flies also benefit from dead salmon; flies consume salmon, lay their eggs and then maggots flourish on dead salmon. You do not see a lot of conservation plans for maggots but the reality is that there is a huge scavenging food web that is associated with salmon carcasses.

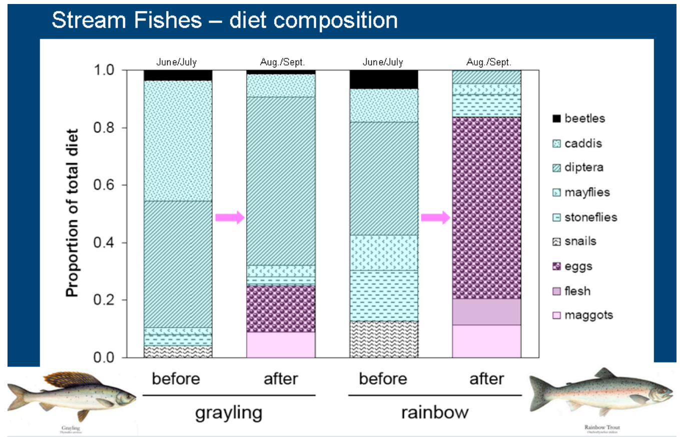

Figure 21. Comparison of diet composition in grayling and rainbow trout in streams before and after salmon (Scheuerell *et al*. 2007).

Of course there are large numbers of fishes that are dependent on salmon resources: for instance, rainbow trout in both BC and Alaska. These rainbows are the focus of very profitable and engaging sports fisheries. The only reason these sports fisheries can exist for resident rainbow trout is due to the annual influx of salmon eggs. When we took a small rainbow trout, with an extended belly and regurgitated its stomach contents, we discovered that the trout ate a lot of sockeye eggs and a few maggots. In a typical stream, this sort of resource is there for three or four weeks of the year. The question is: Is the pulse of energy that is consumed directly from the salmon worth anything to this fish? We have done work addressing this question. Figure 21 compares both grayling and rainbow trout in streams before and after salmon.

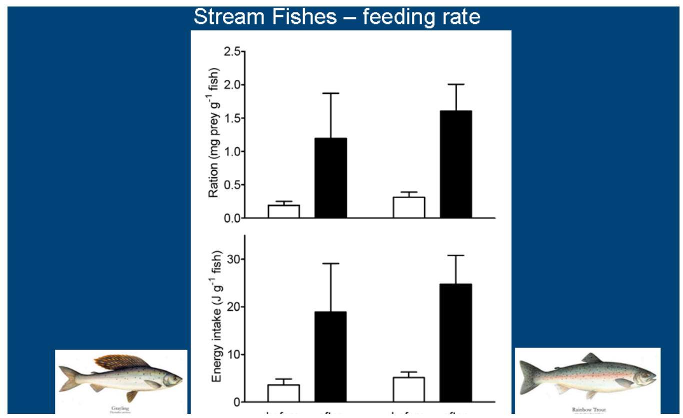

Figure 22. Feeding rates in grayling & rainbows (Scheuerell *et al*. 2007).

In a survey of diets pre and post salmon, what you note in pink are the eggs, flesh and maggots. Diets in both species increase, or there is a change in diets to incorporate some of the direct salmon resources after the fish get in the stream.

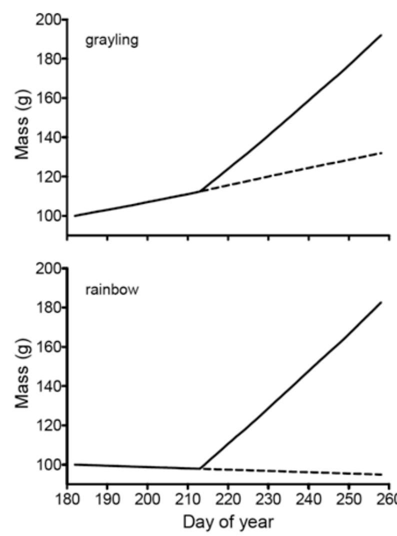

Figure 23. Bioenergetics of grayling and rainbow trout in response to season salmon resource pulses (Scheuerell *et al.* FWB, 2007).

If we convert these to feeding rates, either in terms of energy or biomass, we see that for both grayling and rainbows the daily intake of energy increases four or five times (Figure 22). This is particularly important for energy intake because these eggs are such a high-energy resource.

What does this mean for the dynamics of the consumer? We have not tried to test this with a population model, but we have used a bioenergetics model to ask how it might change potential growth rates. The graphs in Figure 23 represent a bioenergetics model that uses the observed diets and the observed temperature—which turns out to be critical—and then increases in feeding rates as observed when the salmon arrive.

For grayling, not surprisingly, growth rate increases substantially when they start eating salmon resources. For rainbows there is a negative growth throughout the entire year except for when the salmon are present. We have corroborated this for several streams. The point is that many of the streams in Alaska are cold enough that the thermal conditions constrain their ability to grow. The entire annual growth of these fish occurs in a four or five week period and the rest of the year it appears as though the fish are losing mass. If you took salmon out of the system, my guess is that you might lose rainbows altogether or at least reduce them to a few erratic populations.

A spin off on this is to ask: Is this a homogeneous effect or does it vary among years? We surveyed a stream for six years and during that period, the number of sockeye that returned to spawn varied between about 0.1 m^{-2} and almost 1.0 m^{-2}. We also surveyed how many eggs were in the drift of different streams over three years (Figure 24).

If we look at the egg production first, we see these are eggs that are in the drift that would be available to a resident trout, and it is a pretty strong non-linear relationship. In this case, Jon Moore developed an individual based model that showed that the reason for this non-linear relationship is that these salmon are very territorial when they are on the spawning grounds. They move into the spawning grounds, the female digs a redd, releases her eggs, and then defends the redd. The next female comes up and is not going to compete with the original female – she will go and spawn somewhere else. At some point the habitat is saturated and the females start digging up each other's redds through superimposition. At that point, many eggs are produced in the system.

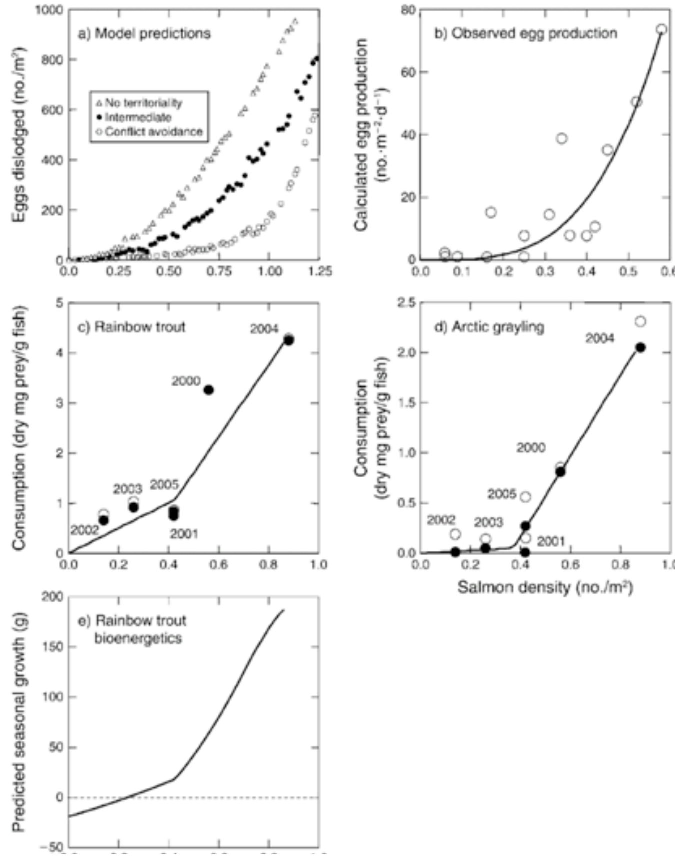

Figure 24. Predation by rainbow trout on sockeye eggs—effect of sockeye density. Should escapement goals for sockeye be changed to account for benefits to sport fishery? (Moore, Schindler and Ruff, Ecology 2008).

In this one stream with rainbow trout and arctic grayling, a threshold of 0.4 m^{-2} fish is reached where suddenly the consumption of eggs increases much more substantially than it does at densities below that. This corresponds to when the system gets saturated with spawners and they start digging up each other's redds and producing more eggs. If we apply a bioenergetics model, we see that below this 0.4 threshold, fish are capable of a slightly positive growth response. However, their growth really does not take off until there are enough fish in the system to saturate the spawning grounds. This is interesting because the fishery managers in this area are managing for MSY for the sockeye and the way we get to MSY is by avoiding density dependence on the spawning grounds. This appears to be an interesting conflict between the needs of the rainbow trout, which seem to require saturation of the spawning grounds and adding a few more sockeye to dig up the redds, versus what you would get under a sockeye-focused, purely MSY type management strategy which would try to avoid too much density dependence on the spawning grounds.

This leads to the question: Should the escapement goals for sockeye be revisited to account for this threshold? Think about the benefits to the sport fishery. The sockeye fishery in Bristol Bay Alaska is very healthy and probably worth about $100-$200 million a year, but it turns out that the sports fishery for rainbows in this area is worth about $100 million a year. Currently, the commercial fish branch of ADFG does all the management on salmon in the system. My guess is that in the next decade the people who manage the sports fishery are going to become an increasingly more powerful voice, and they will gain traction in arguing for higher escapement densities to account for the subsidy to rainbow trout.

In the rainbow trout example, the variation was across time. Figure 25 shows an example where the salmon subsidy, in this case juvenile coho, varied across space. Here Armstrong studied coho growth rates in streams that also have salmon in them. There are four streams, two that are very cold (between 6-8°C) and two that are warm (11-13°C). These are size distributions of juvenile coho at the time that salmon entered the streams. In the cold systems the young coho do not grow big enough to be able to eat sockeye eggs. The 0+ fish are around 50mm and they just cannot get their mouths around a sockeye egg. At the warmer sites the juvenile coho can grow fast enough early in the season so that when the sockeye show up they can capitalize on the egg resource. These are the sites where we get a lot of coho recruitment and it appears to be an effect of the hydrologic template that affects stream conditions and therefore the ability of coho to grow up and be big enough to capitalize on the seasonal pulse of sockeye eggs. Again in this case, the point is simply that we should not expect that the salmon resource should be good everywhere; in some places the community will be able to capitalize on it and in others that is not the case.

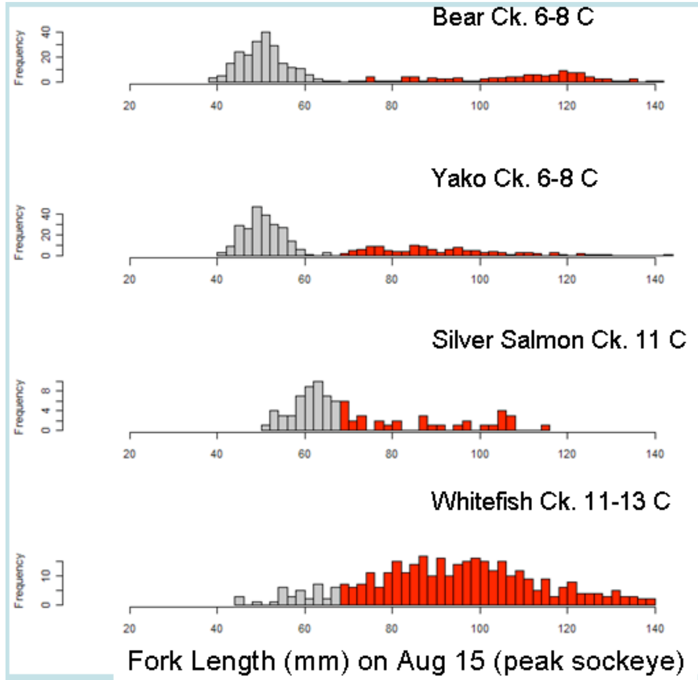

Figure 25. Juvenile coho salmon feeding on sockeye eggs, Bristol Bay, AK (spatial variation in the consequences of the sockeye subsidy) (J. Armstrong unpublished).

There are many other consumers that rely on salmon and there is a lot of work published on this topic. I am not going to discuss this except to say that in many cases I think bears are critical in facilitating predictions about other species.

Salmon effects on riparian productivity

There are a lot of nutrients coming back to streams. Bears eat fish and then do what bears do in the woods and as a result move nutrients into the riparian forest. There are several papers that forcefully argue that it is this key salmon nutrient link that fertilizes the forests and increases their productivity and diversity. Figure 26 provides one such example where the researchers went out to a stream and measured the isotope signature of vegetation either along the stream or by comparing this stream to a reference site.

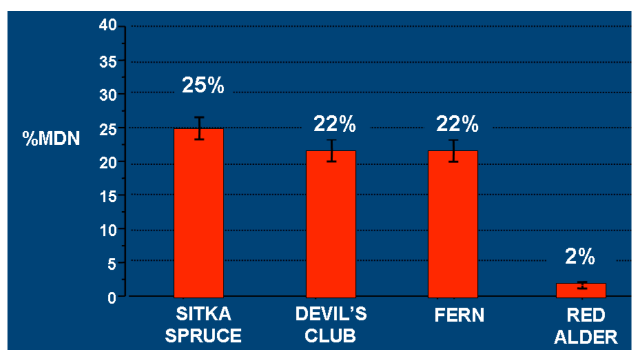

Figure 26. Percent marine-derived nitrogen in riparian foliage at spawning sites, Tenakee Inlet, AK (Helfield and Naiman 2001).

It is often the case that the salmon stream has enriched del-N15 as you think you would see in the presence of salmon. For example, you can calculate how much of the nitrogen in that plant is derived from salmon, and in this study they produced estimates of 20-25 percent. This can then be correlated with the growth of trees.

Research has been conducted in southeast Alaska where sites with spawning salmon have twice the growth rates of sites without salmon. The argument is made that it is this positive feedback that fertilizes riparian habitat and therefore tree growth. I would argue that this body of evidence is fairly weak: correlations are made among riparian systems that have very different biogeochemical processes. Figure 27 shows a transect of nitrate concentrations in groundwater from the edge of a stream backwards up the hill slope and then over the top. Yellow represents the N15 of the nitrogen in nitrate; remember that salmon are bringing in enriched N15. Near the stream you should be getting enriched N15 signatures and in fact you do.

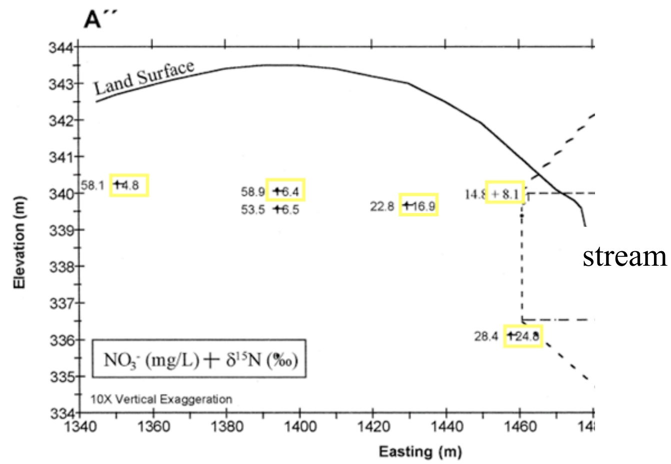

Figure 27. Riparian systems are hotspots of biogeochemical process. Groundwater δ^{15}N isotope values and nitrate concentrations along transect A (adapted from Vidon and Hill 2004).

Near the stream, you see that the N15 in nitrate is between 8 and 25 and it becomes increasingly depleted as you move away from the stream edge. This is the pattern you would expect to see if salmon were the dominant source of nitrogen to the riparian soils. The problem is that this study was done in London, Ontario (i.e., where there is no salmon source of nutrients).

These gradients in N15 in riparian zones are ubiquitous and can be totally independent of salmon. Riparian areas are sites of very strong redox gradients that affect nitrogen cycling, and affect the N15 characteristics of nutrient pools and therefore vegetation. I am not saying that salmon nutrients do not make it into these ecosystems—it is clear that they do, in some cases. However, every estimate of N15 in trees or in vegetation overestimates the importance of salmon because they have ignored these types of effects on isotope fractionation.

These correlative studies are not going to get around this. What we really need to do are experiments where we can manipulate the salmon densities by subsidizing the riparian forest or whatever we want to do and ask how those nutrients are getting incorporated into vegetation. Again the question comes around to determining whether or not the nitrogen isotopes tell you something specifically about ecological dynamics. Right now I would not bet much on the fact that trees in a lot of these areas are actually fertilized by salmon nutrients.

Referring back to the story, the point is that the story is not as good as often told. I don't think it is very useful to managers.

The effects of marine derived nutrients on sockeye salmon productivity appear to us, at least from Alaska sites, to be negligible and the reason is because of density dependence. We need to account for density dependence and about how the population responds to increases in its own density. When we think about streams, we need to think about bioturbation. These salmon are digging up the streambed and that has consequences for the stream, in addition to the salmon nutrients that are released. Salmon are the ecosystem engineers that control many biological and physical processes of streams. Consumers certainly benefit from salmon resources.

What are the important salmon effects in some ecosystems of interest?
I would look first to animals that consume salmon resources directly and in some cases are directly mediated by bears. We do not understand well enough the salmon effects on riparian productivity to implement them in management. They are mostly based on spurious correlations and if this type of work is going to get serious, we really need to do the right experiments. The thing about stream restoration—at least in the US and BC—is that people are taking carcasses from hatcheries and dumping them in streams. This is only satisfying half of the salmon equation. It is not accounting for the fact that salmon are active living animals that dig up the

stream and have all these other effects in the system. If we are going to do this, then I would argue that we should just fertilize the system. Most of these things are pretty burned out and do not have the lipid resource that a live salmon does, especially if a live salmon swims into a stream, gets killed by a bear and then is accessible to caddisflies and other insects.

Acknowledgements
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Discussion:
Question:
There is much in your presentation regarding bioturbation and the sweeping of nutrients and particulate matter out of the system. Was any work done looking at the location of those spawning areas relative to the rest of the watershed and or lake, in terms of whether they were lost as was said or whether they simply are released for reutilization?

Daniel:
They are kicked downstream so the primary producer responses that we see are in the lake and not in the stream. In big river systems my guess is that you get the transport of those nutrients out of areas of intense spawning activity to depositional areas. In a big river, that could be a stretch of the river. In these systems, they are deposited into lakes. Sometimes they take them up and are fertilized by them. You do not see that effect in streams. Certainly, you can imagine various configurations of streams where the spawning habitat may be upstream and the fertilization effect may be downstream. For that to benefit fish you would expect the juveniles would migrate down. There are certainly circumstances like that where the fertilization effect is possible and may be very important. We do not see this in any of the Bristol Bay systems—it may be particular to their geomorphology.

Question:
Would the other consideration there be that the timing is also very site specific?

Daniel:
In these systems, the timing is all over the map. We get fish spawning from the middle of July until the middle of September.

Question:
Certainly implicit in some of your comments is the whole look at limiting factors. We know that there are limiting factors on population dynamics in urban plants and animals—you did not find supporting evidence about that topic in this work. It is not only relevant to the abundance of salmon, but also for the predators that might rely on them such as the grayling and the rainbow trout. You showed evidence that their body size increases, but what does that mean in terms of populations? It seems that this is a general problem with this whole area. There is not just one limiting factor—there are probably multiple limiting factors that increase. In

the case of salmon we know that the marine environment is absolutely critical in determining the total population dynamics.

Daniel:
That is a point that I meant to make. A lot of this research has used isotopes to show that marine derived nutrients make it into consumers. There have been very few studies that have asked: What does it mean for the population dynamics of that recipient pool? Which is what I think what you are getting at. The other issue is: What affects the capacity of all these systems? In this case, at least for sockeye in lakes, we are getting fairly good correlations with historical abundance and what some of the old F.R.I. people did for assessing spawning habitat availability. We get some surprisingly high coherence there. In the Alaska systems, the amount of spawning habitat is a fairly good predictor of how many fish may actually have spawned there in the past. In the case of some of these consumers we have not attempted to do this but this is something that needs to be done. How are the population dynamics of the rainbow trout population going to respond to an egg subsidy? No one has studied this yet, and certainly, it is critical.

Question:
Given that the majority of these examples came from Alaska, I am wondering if there is any reason to suspect, as far as the generality that is given, a wide latitudinal gradient?

Daniel:
There are a number of answers to this. We have looked at wild lakes in British Columbia and it seems as though the nutrient budgets of lakes are swamped by sources of nitrogen other than salmon densities. Salmon densities are just not high enough here to make many meaningful contributions to at least our isotope signatures of sediments but also to the nutrient budgets of the systems. There have certainly been some very high-density salmon coastal streams in British Columbia and who knows what the effects are there. I think there are still going to be nutrient subsidy effects, but the bioturbation effects are also going to be there. How do these things add up? I do not know.

Question:
Your story does not necessarily fit with the sockeye, but you get the impression that with other stream resident fish like coho or rainbow trout they could be benefiting from sockeye spawning. Is there anybody that is actually examining that relationship in terms of the total production of coho and Chinook in real terms?

Daniel:
That again refers to studies where people have ground up the coho salmon and asked how much of these nutrients came from a sockeye, or from a pink salmon. I do not know of anyone who is actually trying to estimate what it means to the population dynamics of that recipient population. The key is probably in cross-species subsidies where large pink or sockeye runs may be critical to coho, Chinook or steelhead populations.

Question:
Nobody has ever done that?

Daniel:
No. That is what I think we need to do and we are fooling ourselves if we think the answer is in the stable isotopes. The stable isotopes just tell you that the nutrients made it into the fish, they do not tell you that it has any effects on the population dynamics, which is ultimately the question that we want answered. That is what management is faced with tackling.

Question:
I want to question the comment you made right near the end of your presentation where you referred to people tossing carcasses into the river and they might be just as well off to put in fertilizer. Basically, you have got the direct consumption pathways and the indirect consumption pathways so that in terms of the critters that would feed directly on the carcasses, which would be all mammals and certain insects, they would probably be less likely to feed on fertilizer than they would on a salmon carcass. There is some benefit, I guess, in terms of putting carcasses into streams, through the direct consumption pathway.

Daniel:
I partially agree with that statement. Again, think about a system that has some relatively natural flux of salmon. One of the things we find with bears is that they kill many of these salmon before they spawn and therefore the quality of the resource available to the scavengers in the community is almost twice what they would get if all those fish spawned out on their own. As the females dig their redds and then defend them for two weeks by the time they die they are basically a bag of ash. They have no lipids left and to a consumer eating them the benefit is much reduced compared to a fish that swims in, and happens to get caught and half eaten by a bear on the first day of entry. The fish that are coming out of a hatchery are burned out as well. Again, I do not think it is the exact equivalent. You are right that there are certainly mammals that will show up and chew on these carcasses but I do not think you can pretend it is the answer to all the problems associated with the loss of live salmon as a source of energy and nutrition for consumers.

Nutrient Workshop Panel Discussion:
There are four panelists: Kim Hyatt is a research scientist and head of the salmon and regional ecosystems program with Fisheries and Oceans Canada. He is intricately involved with the Wild Salmon Policy. Bruce Ward is a fisheries scientist from the BC Ministry of Environment. He has done a lot of work on fertilization around British Columbia and he has an affinity for chum salmon. He calls them the nutrient bags of the salmon world. Rick Routledge is a Professor of Statistics and Actuarial Sciences at Simon Fraser University and he is doing a lot of work on the Central Coast. John Reynolds is the Tom Buell Leadership Chair in Salmon Conservation at Simon Fraser University. Doug Braun is one of John's students working on habitat indicators for sockeye salmon. John has a large team of people working on Wild Salmon Policy issues in British Columbia.

Questions for the Panel:

Looking at variability in salmon nutrient contributions to ecosystems—whether or not they are influenced by in-stream characteristics, salmon species composition and coast versus interior systems:

- What is required for effective implementation of Wild Salmon Policy Strategy 3?
- Which are ecosystem values and the monitoring of these values?
- Can you identify a list of potential indicators of ecosystem health?

Kim Hyatt, Research Scientist and Head, Salmon in Regional Ecosystems Program, Fisheries and Oceans Canada

I am one of the people involved with experimental additions of inorganic nutrients to British Columbia lakes and streams for the last 25 years to see what it actually does to salmon. Consequently, salmon contributions and responses to inorganic nutrient enrichment pathways in aquatic ecosystems are probably as well understood in British Columbia as they are anywhere. The general conclusion from the work of our DFO research group (see Hyatt *et al* 2004 for review) is that freshwater ecosystems throughout the eastern rim of the North Pacific region generally exhibit extreme nutrient limited productivity due to geologic and climatic conditions.

Key inorganic nutrients such as nitrogen and phosphorous are both in short supply because aquatic ecosystems supporting salmon are underlain by a geological foundation of basalt overlain by thin soils that are nutrient poor and heavily leached by high levels of annual rainfall. Consequently, salmon-mediated delivery of production-limiting inorganic nutrients is likely to play an important role in controlling aquatic productivity in many locations. However, contrary to popular mythology, which Daniel has already touched on, salmon-mediated delivery of limiting nutrients is unlikely to be equally important everywhere given geographic heterogeneity in both geology and climate. Thus, interior ecosystems east of the coastal mountains are more nutrient rich than outer-coast systems due to the presence of a drier climate and a more nutrient rich sedimentary geology. We have to take this into account if we are going to start managing salmon harvest or enhancement activities for the impact of marine derived nutrients from salmon on aquatic ecosystem nutrient budgets.

Salmon also import both matter and energy that directly support a diverse predator-scavenger complex in marine and especially freshwater ecosystems about which Daniel has already commented. This salmon-mediated biomass delivery function is harder to replace because although we can throw inorganic nutrients into systems, thus altering their productivity, it is much more difficult to replace salmon as a source of mass and energy consumed directly by the predator-scavenger complex. Moreover, significant portions of this consumed mass ends up in the terrestrial riparian zone compliments of bears that function almost like a squad of “front-end loaders”. Although the relative importance of salmon-mediated inorganic nutrient recycling and direct consumption pathways remains to be defined in space and time, both pathways are recognized as important under Canada’s Wild Salmon Policy (WSP). The WSP obliges DFO to (1) take ecosystem values into account, (2) identify ecosystem objectives as part of salmon management, and (3) set up a system of ecosystem indicators so as to track our performance in meeting these objectives.

For Fisheries and Oceans Canada this means examining our sectoral based activities (e.g. salmon harvest, salmon enhancement, salmon aquaculture and habitat management) for whether they are responsive to our current understanding of the importance of salmon to maintenance of ecosystem integrity. By that, I mean that we need to consider the impacts of sectoral activities that are often concentrated at focal points that alter the distribution and abundance of salmon in watersheds. For example, salmon enhancement may bring back huge quantities of salmon to some areas where mixed stock fisheries then overexploit weaker wild stocks thus producing large changes in the distribution of fish relative to their historical abundance in both space and time. This cannot help but have ecosystem impacts. We have little concrete knowledge about specific ecosystem impacts of these changes and even less idea about what we would do about them. Quantification of both current and historic impacts is necessary if we are to provide prescriptive advice for future sectoral operations management.

Considering major salmon enhancement facilities, I think we really do have some obligations to start to think in terms of adult-to-adult complete cycling systems that recognize the role of salmon-mediated functions in maintenance of ecosystem integrity. Instead of taking biomass away and rendering it for fish pellets that we direct to support aquaculture activities, we may want to look at the consequences of nutrient and energy losses to the predator-scavenger complex and habitats within associated local watersheds and how we might use the nutrients and energy tied up in enhanced adult salmon returns to best effect.

Full implementation of the Wild Salmon Policy will require that we design experimental systems that allow us to quantify the impacts of sectoral activities on ecosystem integrity in the regions where they operate. WSP implementation also requires DFO to become more responsive to dealing with the ecosystem account end of the ledger in terms of fisheries management because we are signatories to both national and international agreements that obligate us to develop an ecosystem approach to fisheries management. Multiple conventions admonish us to avoid doing damage to non-target species. Usually this is thought of in terms of bycatch of non-target species—things such as let’s not destroy steelhead in the pursuit of large net fisheries for sockeye—but you can also think of this in terms of inadvertent damage to the predator-scavenger complex. For example, important BC and Canadian societal values are reflected in the establishment of grizzly bear refuges and national parks where the philosophy is to maintain ecosystems in some kind of normative condition so they remain as close to their primordial state as possible. We may have some special obligations in those locations in terms of how we manage fisheries and other sectoral activities in the future. These obligations will not be met overnight and it is going to take a sound science basis, which we as yet do not have, to arrive at prescriptive operational suggestions for when, where and how to manage sectoral activities to maintain salmon-mediated ecosystem integrity.

We need to do quite a bit more research. Daniel touched on this point in the sense that instead of just following the signature of marine derived nutrients and whether or not MDNs can be found on landscapes or in critters, we really need to create salmon-mediated, energy and nutrient flux models to show quantitatively what the impact of salmon returns are on the integrity (ecological structure and function) of whole communities of organisms. Once created, such models will allow us to compare the importance of nutrient and energy delivery functions of salmon relative to the alternative pathways by which nutrients and energy may be satisfied for whole communities. It will be a non-trivial challenge for fisheries science to provide a clear perspective that allows meaningful headway in specifying salmon management practices to achieve a better balance of ecosystem values for future generations.

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Bruce Ward, Fisheries Scientist, BC Ministry of Environment

It is a pleasure to be here and to see so many students because you have heard, and you will hear again from me, of the need for more research on the topic.

My work on streams began about 35 years ago, with Dr. Kim Hyatt in the UBC Research Forest. I was employed by Dr. Don McPhail to work on rainbow trout and Kim was studying kokanee in Marion Lake. I was also interested in 24-hour insect drift in streams and the territory, food and space requirements in rainbow trout fry, following on the classic territoriality work of Tinbergen (1959) and others in the 1960s. Since there has been much more work done on the question of territoriality. Slaney and Northcote (1974) was classic work that led to further studies on fish abundance, prey abundance, and nutrient levels. Ernest Keeley (1998) followed with more recent work while he was completing his thesis at UBC. Yet there are still many more questions related to fish and prey abundance, marine-derived nutrients, and stream ecosystems to explore, as Dr. Schindler has indicated.

My earlier work lead to a position with the Province of BC working on the Keogh River, on northern Vancouver Island, and studying steelhead trout population dynamics. One of the first key observations we had on steelhead trout smolts was that length frequency and age structure were apparently a function of the odd- and even-year abundance of pink salmon runs (Ward and Slaney 1988). We had no idea (and still don't) whether this was related to the abundance of salmon eggs in the fall and fry in the spring, or subsequent marine-derived nutrient levels as a consequence of the abundance of salmon carcasses. We began pilot experiments on small streams and then whole river experiments to look more closely at the role of inorganic nutrients (surrogate carcasses) in controlling prey abundance and smolt response. Working with Pat Slaney and me were Chris Perrin, and Darcy Quamme, with later work by Ken Ashley and Greg Wilson on the development of the inorganic nutrient material (N and P) itself.

When the stream ecosystem was functioning at its capacity production for steelhead smolts in the mid-1980s—that is, there were abundant steelhead juveniles—it was possible to increase the productivity and capacity by adding inorganic nutrients. Nutrient addition resulted in increased fry numbers and weights and decreased smolt age (Ward and Slaney 1993; Johnston *et al*. 1990). We increased the smolt yield by 1.5 and 2 fold (Ward 1996). However, since then, there have been oceanic regime shifts and climate change (Ward 2000), such that the levels of adult steelhead returns are extremely low. Consequently, fry recruitment is also very low, and food is no longer limiting for these fish. Additional nutrients or carcasses are probably of very little benefit. We have seen no additional benefit to smolt yield in years with added nutrients when the numbers of spawners were <10% of historic capacity (Ward *et al*. 2008). Nonetheless, the pattern of odd-and even-year pink salmon abundance continues, and co-related variable size of steelhead smolts in spring has been retained (McCubbing and Ward 2008). Nutrients can provide a bottom-up response in smolt yield when food is limiting, but it seems that more than marine-derived nutrients or salmon carcasses is of importance to smolt production – the availability of salmon eggs and fry at critical times or seasons may also be a factor.

Time, location and fish community structure are key factors for the Wild Salmon Policy and are related to development of indicators of ecosystem health. The fish community changes with time and location on the coast, in the interior, and within streams. The Keogh example of pink salmon and steelhead trout interactions represents one of many species interactions we have yet to comprehend more fully. Furthermore, stream characteristics interact with the fish community. Thus, the Wild Salmon Policy will need to incorporate ecosystem management and indicators of ecosystem health; work that has only just begun. There is much more research required before there might be a clear focus on good indicators of ecosystem health. Add to this the present and impending climate change challenge. To address climate change, there is a need to not only monitor survivals, but also to develop riverine, estuarine, coastal, and ocean ecosystem models to predict and test climate change hypotheses concerning limits within salmonid life stages (freshwater, during migration, coastal seas, or ocean life history period) and controls on the abundance of anadromous coastal and interior fish species, and then to develop mitigation strategies for wild fish if, when, and where possible. Steelhead trout amalgamate freshwater, migratory, coastal, and ocean effects in their complex life history, and thus are the harbinger to society on the enormity of the issues, the difficult analyses of impacts, and the complexities of the solutions and management options. These trout are thus also well-suited to act as indicators of ecosystem health.

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Rick Routledge, Professor, Statistics and Actuarial Sciences, Simon Fraser University

I would like to make two comments about latitudinal gradients, an issue that was raised earlier in a question. First, there is a lot of scope for big latitudinal gradients as it appears to me. Daniel gave a very interesting presentation on the impact of slightly warmer temperatures on coho salmon growth rates. Of course we have much more water down here. Also we have a much later spawning season. Coho salmon are probably spawning right now—chums were spawning just a month or two ago and that is going to impact those dynamics quite substantially. We also have a much more humanized version down here and that is governed by complex human interactions that Daniel described with respect to human interactions and forestry.

One thing that came home to me in the course of Daniel's talk was how complicated the natural ecosystem is compared to an eves trough with some carcasses in it—and the notion of downstream impacts came up several times. I would like to relate a story about my work in Rivers Inlet in the Central Coast where we took sediment cores out of some lakes and measured the N15 as well. We discovered a few surprises, some of which we still do not understand. One was that there was no immediate drop in the N15 in the lake sediments concurrent with the onset of the fishery. It took several decades for it to really start to show up. Yet at the same time that the fishery started up you can see an immediate response in some of the zooplankton indicators. So it looks like the fish gradation, the reduction in juvenile gradation, was an immediate impact but yet somehow the N15 signature did not change. We do not really understand that—we have some ideas, but I cannot say that they are definitive.

One other important thing that I want to mention is that we took some cores out of this lagoon as well and found evidence of simultaneous changes in the lagoon that match what was happening in the lake. That lagoon is clearly critical habitat for small sockeye salmon smolts when they come out. Early in the season, we caught larger juvenile sockeye salmon migrating relatively rapidly through the inlet. We found the smaller ones hanging around in Wyclees Lagoon until well into the summer. Hence, the lagoon, with its brackish surface layer appears to be an important staging area for the smaller fish. Our preliminary examination of the sediments from the lagoon showed that the changes in the lake were mirrored in the lagoon.

Maybe the same thing is happening in the Strait of Georgia. All these salmon carcasses that have been deposited up in the lower Fraser are not going to be in the streams once the big rain storms come. Maybe the nutrients are washed down into the Strait of Georgia and that is where the important impacts are.

John Reynolds, Tom Buell Chair in Salmon Conservation, Simon Fraser University

I would like to thank Daniel Schindler for a very thought-provoking presentation of his excellent research program. I will try to structure my comments around the questions that were posed for us by the organizers with respect to ecosystem considerations for implementing Canada's 2005 Wild Salmon Policy. This will include some comparisons between Daniel's findings in Alaska and our studies in British Columbia.

Strategy 3 of Canada's Wild Salmon Policy attempts to link salmon to ecosystems, recognizing that salmon may underpin healthy ecosystems by serving as food for other species or providing fertilizer to plants in streams, riparian zones and estuaries. The policy does not define "healthy ecosystem", but sums up the dilemma succinctly:

> *A challenge for the Wild Salmon Policy is the need for development of an ecosystem objective that is widely appreciated but difficult to quantify.*

To come up with workable definitions of "healthy ecosystem", supported by indicators, is a major research program by itself. This is not just a scientific question. In my reading of the Wild Salmon Policy, I get the impression that the "values" that it refers to include aspects of ecosystems that people value. I think the scientific search for a definition of "healthy ecosystem" may be complemented by some sort of public process to ask people what aspects of ecosystem health they care about with respect to the role of salmon.

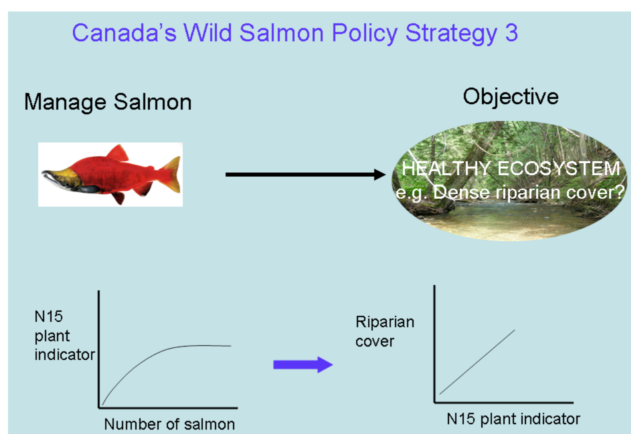

Figure 1. A hypothetical indicator that links abundance of salmon to ecosystem health. The objective could be a certain density of riparian cover, and the indicator could be the amount of N15 in plant leaves, which has been derived from salmon. Sockeye illustration courtesy of Joseph R Tomelleri, stream photo by Doug Braun.

How might salmon, indicators, and healthy ecosystems fit together in a way that we can measure? Suppose we use an operational definition of "healthy ecosystem" as "dense riparian cover" (Fig. 1). We might develop benchmarks for how dense we want the cover to be, and we would probably add various caveats, such as wanting native species, with some level of diversity among species.

How would we indicate this, and its linkages to salmon? Perhaps a stable isotopic nutrient signature could be found in a species of plant that relates directly to the number of salmon (Fig. 1 left graph). If that indicator in turn was correlated with riparian cover, then we could simply collect leaves from our plant and process its isotopes of nitrogen, and we would have the link between how many salmon there are and how "healthy" the ecosystem is. Targets for salmon escapement could then be set according to specific benchmarks of this aspect of ecosystem health, which would need to be tailored to the salmon carrying capacities of streams. Progress toward the target could be assessed by counting salmon and collecting leaves, which can take far less time than surveying vegetation plots.

An example that illustrates the left graph of Figure 1 is in Figure 2, from a study by Nagasaki *et al*. (2006), from streams in Hokkaido, Japan and nearby Etorofu Island, in Russia.

This shows that the heavy nitrogen signature in willow leaves reaches a maximum at carcass densities of about 1,500 salmon per km. The authors warned that some of this variation may have reflected denitrification, or nitrogen fixation by alders, which is an issue that Daniel warned us about, and which can be tackled most easily by using non-salmon reference sites, as is typically done. In our research in BC's Central Coast, we also get these sorts of asymptotic relationships between salmon densities and N15 in plants. Our focus is on taking it to the next level, to consider whether the relationships indicate changes in biodiversity, measured not only as density of plants, but also with respect to specific species of plants that we expect to benefit most.

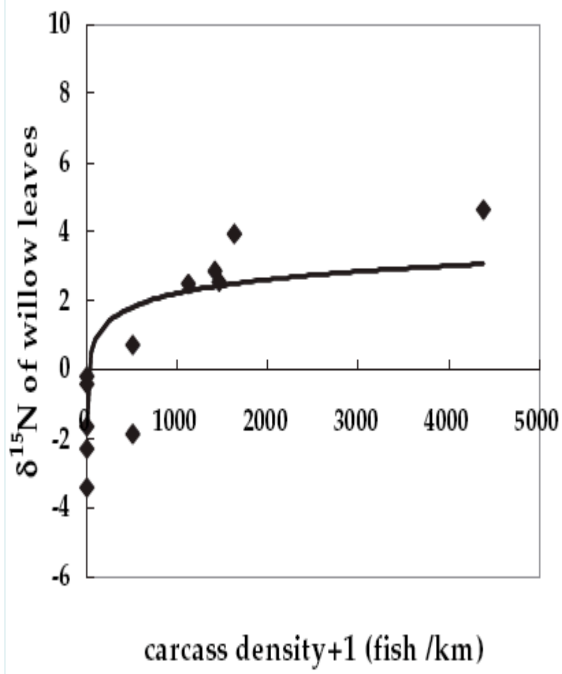

Figure 2. An example of the hypothetical indicator shown in Figure 1: N15 in willow leaves versus densities of salmon in different streams in Hokkaido & an adjacent island in Russia. (Nagasaka *et al*. 2006).

Daniel's presentation touched on an issue that I have also been thinking about, which is that it is possible to have indicators that are also objectives. An objective can be much less nebulous than a "healthy ecosystem". It might be a certain number of bears, if that is an ecosystem "value" that we care about. Bears could be both an indicator of a healthy ecosystem and an objective. In that case all you need to know is the relationship between the number of bears and number of salmon. For example, research by Tom Quinn and colleagues in the same Alaskan Salmon Program that Daniel participates in, has shown that about 10,000 salmon per hectare support maximum rates of predation by grizzly bears (Quinn *et al.* 2005). The Wild Salmon Policy could manage salmon to targets such as this (Figure 3), and test success by counting fish and bears, without the need for an intermediary indicator such as a stable isotope signature illustrated in my first example in Figure 1.

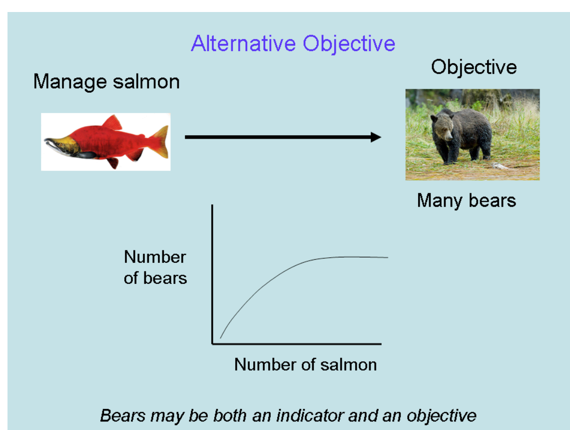

Figure 3. An alternative scenario to Figure 1, illustrating that some species such as bears could be both an indicator & an objective. Grizzly bear photo: Andrew Wright.

Daniel's presentation got me considering another important issue for the Wild Salmon Policy, which is whether specific ecosystem indicators will work in different regions.

The photos we just saw of Alaskan streams showed minimal riparian cover, no large trees in the streams, and uniform gravel. Frankly, they looked like artificial spawning channels compared with the streams we work on around Bella Bella in the Great Bear Rainforest in BC's Central Coast. I can understand why many nutrients will be washed out of these systems by the digging action of salmon, and these might not be offset very much by carcass decomposition, because there is little in the streams to keep carcasses from washing out.

Contrast that sort of northern stream with the streams my research team studies in the Central Coast region of BC. (Fig. 4). I suspect there is far more carcass retention in these heavily forested regions than in the Alaskan systems.

Figure 4. Hooknose Creek, near Bella Bella on the Central Coast of BC. Photo: JD Reynolds.

If so, then salmon may have a more positive influence on nutrients in forested areas than in the Alaskan systems. This issue is related to the earlier question about whether nutrients in Alaskan streams are just transported somewhere else in the stream (or the lake that the stream feeds into), rather than being lost from the entire freshwater system. We need to learn more about how stream-specific the potential impacts of salmon are as ecosystem engineers. In the meantime, I would be cautious about generalizing from the Alaskan systems to those further south.

Another consideration in generalizing from one area to the next about impacts of salmon on ecosystems is the strength of predation pressure. A large population of bears could remove carcasses from the streams (and deposit them inland), whereas if there are fewer bears, more carcasses could be able to accumulate in pools and behind obstructions, as we typically see in the Central Coast of BC. We do not have estimates of bears and predation pressure yet, and we will also need to consider wolves, which can take a lot of fish from the lower reaches of some of the streams. Linking the impacts of different predators on freshwater and terrestrial biodiversity is a high priority.

In conclusion, I thank Daniel Schindler for framing the issues surrounding the role of salmon in ecosystems. We clearly have some challenges in managing salmon for those linkages, but I feel that we are already in a position to identify the key linkages, and choose appropriate ecosystem indicators. In 2005 the Wild Salmon Policy stated: "Within two years, an ecosystem monitoring and assessment approach will be developed and integrated with ongoing assessments and reporting on the status of wild salmon." I hope the Department of Fisheries and Oceans will be able to deliver the resources and person power to do this sooner rather than later.

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Discussion:

Question:

We had a peripheral discussion about the issue of geographical location and the applicability of the research. For those of us that are working on urban watershed conservation basically everything gets thrown out the window because we have got huge influences on nutrients inputs into the system. Marine derived nutrients may have no real impact on the systems anymore versus what they have had historically. Obviously in many areas there is a conflict between natural predators, so in many instances the natural predators are actually gone. On top of that there is the issue of wild salmon conservation and the application of hatchery inputs in terms of systems that may not be looking at what the actual nutrient balance of the system should be and what the carrying capacity of the system should be.

John Reynolds:
It is important to remember that we can only do so much with salmon. Salmon are the management tool that we are trying to deal with in the Wild Salmon Policy. Given that everything has changed—even the Central Coast sites are not pristine in any sense—I think all you can do is think about what would be achievable with a reasonable density of spawning fish. What could that ecosystem look like? As Bruce noted, with these changed oceanic conditions many of the streams are so far below anything like a carrying capacity that in many ways it is almost a moot point. The objective of trying to bring fish back is the same as having more nutrients in the system. We do not have the luxury of asking whether we should have more fish die, so to speak. Many of us working with urban streams would be happy just to see a self-sustaining salmon population.

Bruce Ward:
This question raises the important point of the decision-making process and what the objective is in the first place. What prescription must we apply to achieve the objective if it is at all possible? Some focus on that subject alone is required, let alone the subject of whether the densities are high enough to elicit a response.

Rick Routledge:
It is an issue in fact of what we can do. There are systems which we can reengineer for such profoundly different structure and cultural problems that they are not going to return to a pristine state. First, you had processes that lead to that in the first place, either engineered by intent or by default. Those processes in urban environments are still there. You essentially convert this to an urban environment to meet human objectives that did not include placing a high priority on maintaining an undisturbed natural state. Now you can look at these situations and say "how much normative function and structure can be restored?" with as much effort as the community is willing to invest in it, and then decide whether or not that kind of normative structure and function is pleasing enough to pursue. I work in the south Okanagan where an entire river, the Okanagan River, is currently 50% of its original undisturbed length because it is channelized and is arrow straight through the whole channel. It is costing around $3-4 million per .05 km to create setback dikes and slight meanders and a visual appearance of something that is aesthetically more attractive and possibly more functional for salmon and critters. That is a huge price, but they are willing to pay for a piece of it. That leaves, by my estimation, around 95.5 km still to be dealt with. Multiply that by $4 or $5 million and this is a very significant cost.

Question:
I want to explore a point that both Rick and Daniel mentioned. In one of Daniel's slides, there was a graph with the nutrient load and the salmon abundance and it looked like there was about a ten-year lag in the peaks. Rick said he saw almost the same thing—a ten year lag between marine derived nutrients and salmon abundance. How can you explain that?

Daniel Schindler:
There are two reasons. The first one is the escapement numbers are not reliable from the turn of the century—in fact I do not like comparing numbers prior to 1960. The other reason is that there probably are some nutrients tied up in these watersheds.

Rick Routledge:
One explanation is that the escapement did not actually drop right away—that there was a natural increase in the returns of fish at the time. We have no escapement data at all, not even how many. We do not even have good catch statistics for the creel fisheries. If we think hard about it, it actually was not a 10 year delay—it was more of a 30 year delay so we think that might account for part of it.

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