Fish as Fertilizer: The Impacts of Salmon on Coastal Ecosystems

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General Background

Movement of Nutrients in Ecosystems

An important characteristic of ecosystems is the movement of nutrients (elements contained in molecules, e.g., C, N, P, and others) among components of an ecosystem and between different types of ecosystems. Much of the physical movement of nutrients is driven by the movement of water, which carries nutrients both directly dissolved in the water and as particles carried along in the flow. This water-mediated movement is powered by gravity and so is largely one way, downhill or downstream, in most cases ultimately ending in the ocean.

There are, however, some important examples of reversals of this flow of nutrients. For example, river floods can redistribute nutrient-rich sediments back "up-hill" onto what is in other conditions dry land. In the Pacific Northwest of North America, spawning salmon move from the ocean back upstream into freshwater. Scientists suspect that this salmon migration functions as a nutrient "conveyor belt," carrying marine nutrients back into freshwater and even to surrounding terrestrial ecosystems.

In this case study, you will examine evidence from a growing body of research investigating the role of Pacific salmon in ecosystems in and near where they spawn. The figures examine the movement and impact of salmon-delivered nutrients in the stream and riparian (= streamside) ecosystems. Before you begin examining the data yourself, you should familiarize yourself with the basic life cycle of Pacific salmon and the techniques scientists use to track the nutrients salmon deliver by reading the sections below.

Pacific Salmon Life Cycle

There are five species of Pacific salmon (genus *Oncorhyncus*) that spawn in northwestern North America: chinook *(O. tshawytscha)*, sockeye *(O. nerka)*, pink *(O. gorbuscha)*, chum *(O. keta)*, and coho *(O. kisutch)*. Although they vary in the details of their life history and ecology, all five species share a general life cycle.

A Pacific salmon starts life as a pea-sized egg laid in a nest or ***redd***, a shallow depression excavated from the gravel bottom of a stream (or sometimes a lake) by the mother. After a period of development, the egg hatches as an ***aelvin***, which remains attached to the yolk and buried in the gravel until the yolk is completely absorbed. The salmon is then a ***parr***, which spends weeks or months in the stream feeding and growing. When ready, the young salmon, now a ***smolt***, heads downstream, undergoing physiological changes necessary for the switch to marine conditions. A salmon spends one or more years in the ocean, where it gains > 95% of its final body mass by eating crustaceans, fish, and other marine animals.

At sexual maturity, salmon migrate in some cases long distances through the ocean and then travel upstream, without feeding, to return to the same area where they were born. Along the way and at spawning sites, many salmon are captured by predators such as eagles, seals, bears, and humans; terrestrial predators such as bears and birds often move a captured salmon to land before consuming all or part of it. At the spawning site, a female excavates a redd, then releases her eggs over it; at the same time, the dominant male in the area releases sperm over the eggs. The fertilized eggs settle into the gravel at the bottom of the redd, and the life cycle starts again.

After spawning, the adult salmon soon die, depositing 2–20 kg (sometimes up to 50 kg!) each of organic material (biomass) in the streams at or near the spawning site. Carcasses are eaten by aquatic scavengers, terrestrial scavengers (such as bears, other mammals, and birds, which sometimes move carcasses to land), or microbial decomposers. Since most of this biomass is from growth that occurred in the ocean, and spawning runs in a single river system can number in the tens of millions, this represents a huge amount of ocean-derived organic material being transported upstream into freshwater and the surrounding riparian ecosystems.

In summary, Pacific salmon share three important life history characteristics: ***anadromy***, starting life in freshwater, moving to the ocean, then returning to freshwater to reproduce; ***homing***, returning to the natal stream to reproduce; and ***semelparity***, reproducing once and dying (as opposed to ***iteroparity***, having more than one reproductive bout during the life cycle).

Stable Isotope Analysis

Simple observation of salmon spawning runs reveals that large amounts of marine-derived organic material is being deposited in and around spawning streams. But do these organic molecules of marine origin (marine-derived nutrients, or MDNs) actually get into these upstream ecosystems, and, if so, what parts? Scientists studying these questions have been able to trace the path of salmon-delivered MDNs using stable isotope analysis.

Many elements have different isotopes, which are versions of the element with different atomic weights because they have different numbers of neutrons in the nucleus. ***Unstable*** isotopes are radioactive (emit atomic particles) and change from one isotope to another; these are not what we are interested in here. Many elements important in organic molecules have one or more ***stable*** isotopes (i.e., they ***don't*** change into other isotopes). The two elements most important to the study of MDNs are nitrogen and carbon, both of which have two stable isotopes—^{14}N and ^{15}N, ^{12}C and ^{13}C (the superscripted number refers to the atomic weight of the isotope). For both elements, the heavy isotope is much less abundant than the light version (less than 2% of molecules). However, the ratio of the two isotopes is not uniform throughout the Earth. This is because physical and biological processes can select among (or fractionate) isotopes of different weights. For example, evaporation discriminates against heavy isotopes. On the other hand, heavy isotopes of nitrogen tend to accumulate in consumers (relative to what they eat). The result is that different ecosystems and different components of ecosystems will have different ratios of heavy: light isotopes of some elements. The isotopic ratio of a sample of say a fish or a plant can be measured using a technique called mass spectroscopy.

The key to tracing MDNs is that the oceans tend to be enriched in heavy isotopes of nitrogen and carbon relative to freshwater or terrestrial ecosystems. The bodies of salmon returning to streams to spawn likewise have higher heavy: light isotope ratios than their surroundings. This means that scientists can trace the path of MDNs in stream and riparian ecosystems by looking for enrichment of the heavy isotopes ^{15}N and ^{13}C.

In ecological studies, isotopic ratios are usually presented as δ (delta) values, which are differences in ratios between a sample (e.g., a salmon) and a reference standard, usually given in parts per thousand (‰). For example, for nitrogen, δ would be calculated as:

$\delta^{15}N$ = (R sample – R standard) / R standard × 1000

where R = the ratio of ^{15}N:^{14}N. Because the standard typically used for calculating $\delta^{14}C$ has a relatively high ^{14}C:^{13}C ratio, $\delta^{14}C$ values usually are negative. For both N and C, higher delta values mean higher amounts of the heavy isotope; so higher $\delta^{15}N$ or $\delta^{14}C$ is an indicator of enrichment from marine sources.

Part 1—Do Salmon Add Marine-Derived Nitrogen to the Stream Ecosystem?

Instructions

Turn to your neighbor (or with a small group) and work together to first describe and then interpret the data in the two figures. Use the Step 1–Step 2 approach described below to interpret the two figures.

- *Step 1:* Describe the graph and what it shows. Make sure you understand how the figure is set up, what the axes show, and what information is depicted. Carefully describe the overall patterns in the data.
- *Step 2:* Try to interpret the data. What do they tell you about the effect of salmon on marine-derived nutrient levels in the stream ecosystem?

When you understand the figures, try to answer the questions about the figures. Be prepared to volunteer or be called on during our class discussion to explain a figure or share your answer to a question.

Figure 1—Background

From: Bilby, R.E., B.R. Fransen, and P.A. Bisson. 1996. Incorporation of nitrogen and carbon from spawning coho salmon into the trophic system of small streams: Evidence from stable isotopes. *Canadian Journal of Fisheries and Aquatic Science* 53:164–173. Used with permission.

Nitrogen and carbon stable isotope ratios were measured in aquatic organisms collected from a stream with spawning coho salmon (Grizzly Creek) and one lacking salmon (Stream 0372) because of an impassable waterfall. Apart from the presence or absence of salmon, the two streams are physically and ecologically similar. Both are small (4–6 m wide) with a pool-riffle morphology and similar riparian vegetation.

Samples at each site included epilithic organic matter (the film encrusting rocks in the stream composed of microbes such as bacteria, algae, and fungi), aquatic invertebrates, and cutthroat trout. Invertebrates were classified into 4 trophic (feeding) categories (shredders, grazers, collector-gatherers, and predators) but, because of seasonal scarcity of some types, only grazers (animals that scrape organic material from rocks) and predators are shown here. Samples were collected in the winter (just post-spawning) and early autumn (just before spawning) to examine seasonal variation in isotope

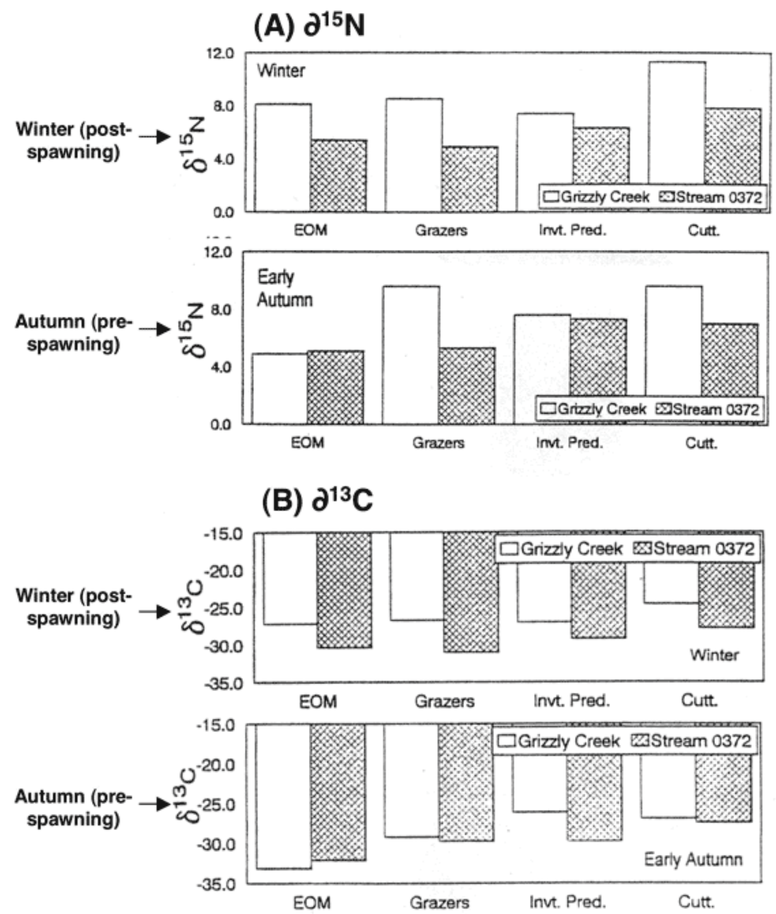


Figure 1—Difference in $\delta^{15}N$ (A) and $\delta^{13}C$ (B) values between Grizzly Creek (open bars—with salmon) and Stream 0372 (shaded bars—no salmon) for four trophic levels (epilithic organic matter (EOM), grazers, invertebrate predators, and cutthroat trout) during the winter (just post-spawning, carcasses present in Grizzly Creek) and early autumn (just ***pre-spawning***, carcasses absent from all streams).

ratios. Remember that, for both N and C, a higher δ value (less negative in the case of C) is indicative of marine-derived nutrients (MDN).

Figure 2—Background

From: Chaloner, D.T., K.M. Martin, M.S. Wipfli, P.H. Ostrom, and G.A. Lamberti. 2002. Marine carbon and nitrogen in southeastern Alaska stream food webs: Evidence from artificial and natural streams. *Canadian Journal of Fisheries and Aquatic Sciences* 59:1257–1265. Used with permission.

This study was designed to determine if marine-derived nutrients (nitrogen and carbon) from dying adult salmon ended up in stream fish, in this case juvenile coho salmon. The experiment was conducted in 36 artificial stream channels (250 cm long, 18 cm wide) gravity-fed with water from a nearby stream. The artificial streams were open to colonization by microbes and small animals (e.g., aquatic insect larvae) brought in by the water. Each artificial stream contained 3 juvenile coho salmon and 0–4 adult salmon carcasses, depending on the randomly-assigned treatment. After about 10 weeks in the artificial stream channels, a tissue sample was taken from each juvenile salmon for stable isotope analysis.

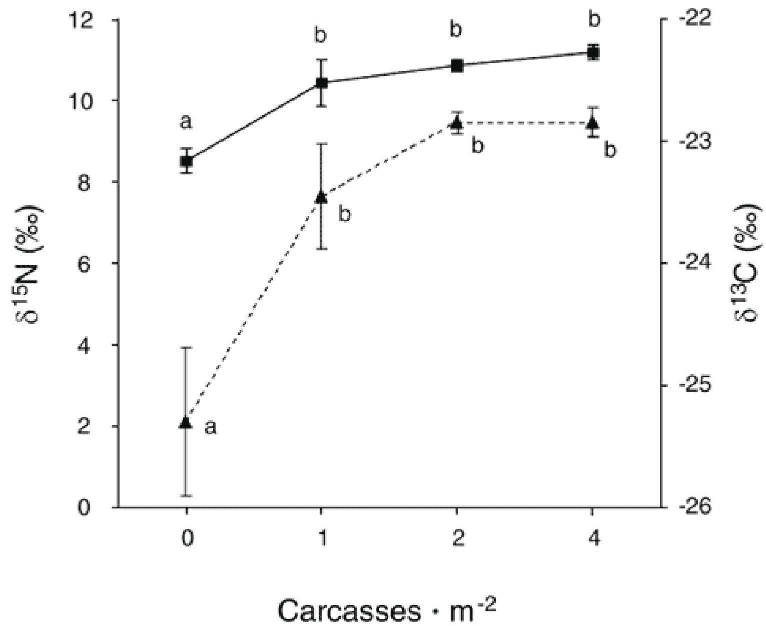


Figure 2—Mean $\delta^{15}N$ (black square values on L vertical axis) and $\delta^{13}C$ (black triangle values on R vertical axis) (± 1 standard error; n = 3) values for juvenile coho salmon after 10 weeks in artificial stream channels containing different numbers of salmon carcasses (horizontal axis). Different letters above the symbols indicate statistically significant differences between treatments (number of carcasses).

Questions

1. Do marine-derived nutrients (MDNs) from salmon get incorporated into the stream food web? If so, what parts (trophic levels or feeding categories)? Refer specifically to the data in the figures to support your answer.
2. (a) What is the significance of looking at both N and C stable isotope ratios? (Think about—or review, if you can't remember them—how the biogeochemical cycles of these two elements differ, particularly in how they move within a food web.)

   (b) Compare the patterns of N and C in Figure 1. What does this tell us about how the MDN are entering the food web?
3. What do the seasonal changes in enrichment (Figure 1) tell us about the source of the MDN?
4. Both studies measured MDNs in fish. Aside from examining different species, does the experiment (Chaloner et al. 2002; Figure 2) tell you anything different than the observational study (Bilby et al. 1996; Figure 1)? If so, what?

Part 2A—Do Marine-Derived Nutrients Affect Stream Organisms?

Instructions—First Jigsaw Group

Read the background information for your figure carefully, then work with your group to understand the figure or figures in the section you are assigned. Use the Step 1–Step 2 approach described below.

- *Step 1:* Describe the graph and what it shows. Make sure you understand how the figure is set up, what the axes show, and what information is depicted. Carefully describe the overall patterns in the data.
- *Step 2:* Try to interpret the data.

When all of the members of your group understand the figure, work together to answer the accompanying questions; they will help guideyou as you interpret the graphs and make conclusions. Write down anything your group still doesn't understand (ask for help from your instructor if needed).

Next, prepare to help the rest of the class understand what you just learned. Think about how you can best explain the graph (its elements and what it shows) and your conclusions to other students who are seeing it for the first time. Be sure everyone in your group is ready to explain your figure(s).

Figure 3—Background

From: Wipfli, M.S., J. Hudson, and J. Caouette. 1998. Influence of salmon carcasses on stream productivity: Response of biofilm and benthic macroinvertebrates in southeastern Alaska, U.S.A. *Canadian Journal of Fisheries and Aquatic Science* 55: 1503–1511. Used with permission.

To determine the patterns of biofilm (microalgae, bacteria, and fungi attached to rocks) and macroinvertebrate abundances in a natural stream, rocks were sampled at two sites on Margaret Creek near Ketchikan, Alaska, during the fall spawning season. (Macroinvertebrates are animals without backbones that are large enough to see without magnification; juvenile insects are the most common in fresh water.) The carcass-enriched site was a salmon spawning area (75,000 salmon spawn in the creek annually) with abundant salmon carcasses. The control site was upstream of salmon spawning and contained no salmon carcasses. Biofilm (sometimes called epilithic organic matter, or EOM) abundance was measured as ash-free dry mass (AFDM): a sample is dried, weighed, oxidized (incinerated) in an oven, and reweighed. The difference in weights is AFDM, a measure of the organic material in the sample.

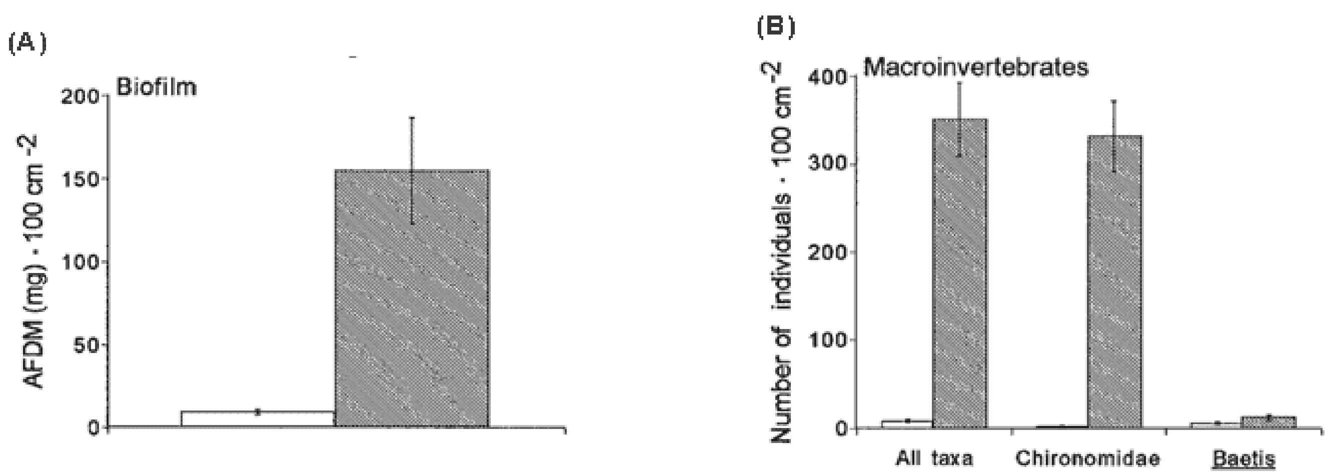


Figure 3—Mean (± 1 standard error) biofilm AFDM (A) and benthic macroinvertebrate densities (B) on stone surfaces within Margaret Creek, comparing upstream control (no salmon carcasses—open bars) and downstream (with salmon carcasses—shaded bars) areas. In (B), data for the two most abundant subgroups of macroinvertebrates are also shown. Chironomidae = midge larvae (Order Diptera); Baetis = a genus of mayflies (Order Ephemeroptera).

Questions

1. Does the presence of salmon carcasses affect the abundance of biofilm or macroinvertebrates? Support your answer by referring to specific data in the figures.
2. Based on these results, what effect do you predict salmon carcasses would have further up the stream food chain (e.g., on predators of macroinvertebrates such as fish)?

Part 2B—Do Marine-Derived Nutrients Affect Stream Organisms?

Instructions—First Jigsaw Group

Read the background information for your figure carefully, then work with your group to understand the figure or figures in the section you are assigned. Use the Step 1–Step 2 approach described below.

- *Step 1:* Describe the graph and what it shows. Make sure you understand how the figure is set up, what the axes show, and what information is depicted. Carefully describe the overall patterns in the data.
- *Step 2:* Try to interpret the data.

When all of the members of your group understand the figure, work together to answer the accompanying questions; they will help guideyou as you interpret the graphs and make conclusions. Write down anything your group still doesn't understand (ask for help from your instructor if needed).

Next, prepare to help the rest of the class understand what you just learned. Think about how you can best explain the graph (its elements and what it shows) and your conclusions to other students who are seeing it for the first time. Be sure everyone in your group is ready to explain your figure(s).

Figure 4—Background

From: Wipfli, M.S., J. Hudson, and J. Caouette. 1998. Influence of salmon carcasses on stream productivity: Response of biofilm and benthic macroinvertebrates in southeastern Alaska, U.S.A. *Canadian Journal of Fisheries and Aquatic Science* 55: 1503–1511. Used with permission.

The researchers conducted an experiment in 36 artificial flow-through stream channels with natural substrate. Each artificial stream was set up to include a deeper pool habitat and a shallow "riffle" habitat. Macroinvertebrates colonized by drifting with the inflowing water. (Macroinvertebrates are animals without backbones that are large enough to see without magnification; juvenile insects are the most common in fresh water.) In half of the channels, one salmon carcass was placed in the upstream end. To sample macroinvertebrates, small-mesh nets were placed over the outflow and the substrate (rocks and gravel on the bottom) in one section of the artificial stream was agitated.

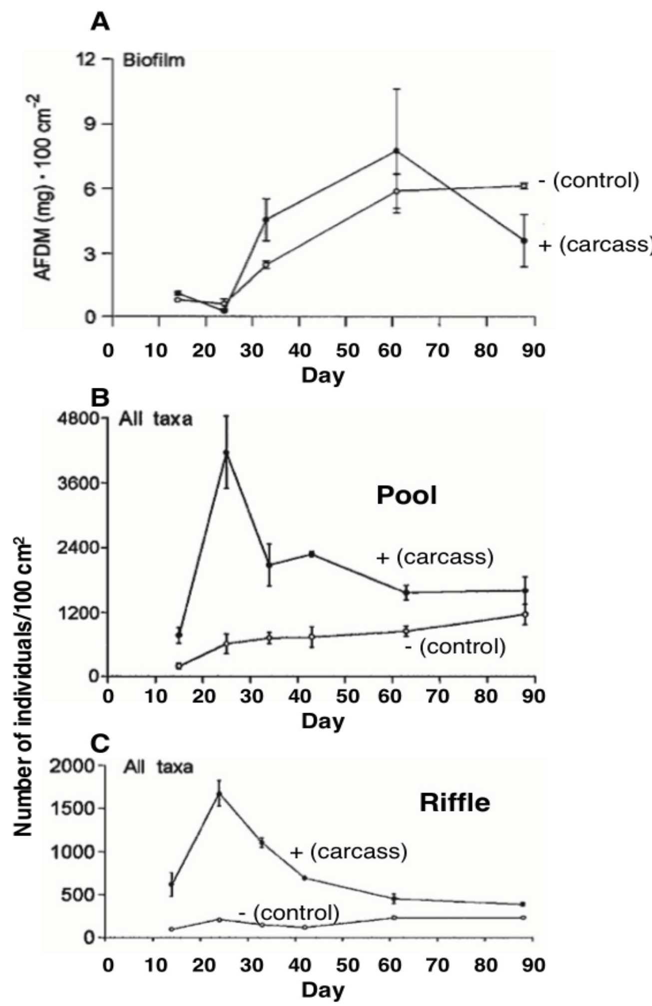


Figure 4—Mean (± 1 standard error) biofilm AFDM (ash-free dry mass) (A) and macroinvertebrate densities in pool (B) and riffle (C) habitats in artificial stream channels, comparing carcass-enriched (solid circles) with control (open circle) treatments over the course of the 87-day experiment.

Biofilm was sampled from an unglazed clay tile at the downstream end of the artificial stream. Biofilm (sometimes called epilithic organic matter, or EOM) abundance was measured as ash-free dry mass (AFDM): a sample is dried, weighed, oxidized (incinerated) in an oven, and reweighed. The difference in weights is AFDM, a measure of the organic material in the sample.

Questions

1. Does the presence of salmon carcasses affect the abundance of biofilm or macroinvertebrates? Support your answer by referring to specific data in the figures.
2. Based on these results, what effect do you predict salmon carcasses would have further up the stream food chain (e.g., on predators of macroinvertebrates such as fish)?

Part 2C—Do Marine-Derived Nutrients Affect Stream Organisms?

Instructions—First Jigsaw Group

Read the background information for your figure carefully, then work with your group to understand the figure or figures in the section you are assigned. Use the Step 1–Step 2 approach described below.

- *Step 1:* Describe the graph and what it shows. Make sure you understand how the figure is set up, what the axes show, and what information is depicted. Carefully describe the overall patterns in the data.
- *Step 2:* Try to interpret the data.

When all of the members of your group understand the figure, work together to answer the accompanying questions; they will help guideyou as you interpret the graphs and make conclusions. Write down anything your group still doesn't understand (ask for help from your instructor if needed).

Next, prepare to help the rest of the class understand what you just learned. Think about how you can best explain the graph (its elements and what it shows) and your conclusions to other students who are seeing it for the first time. Be sure everyone in your group is ready to explain your figure(s).

Figure 5—Background

From: Wipfli, M.S., J. Hudson, and J.P. Caouette. 2003. Marine subsidies in freshwater ecosystems: Salmon carcasses increase the growth rates of stream-resident salmonids. *Transactions of the American Fisheries Society* 132: 37–381. Used with permission.

This study measured the effects of salmon carcasses on the growth rates of fish using both laboratory and field experiments. Growth rates of young coho salmon were measured in 36 artificial stream channels stocked with different numbers of salmon carcasses. Artificial streams contained stream gravel and received stream water flow for 26 days prior to the experiment to ensure colonization by macroinvertebrates. (Macroinvertebrates are animals without backbones that are large enough to see without magnification; larval insects are the most common in fresh water.) Growth rates of cutthroat trout from sections of natural streams with or without experimentally-added salmon carcasses were measured for individuals that were marked and recaptured on two dates. In the "addition" stream sections, salmon carcasses were added on 5 dates to simulate the natural pattern of salmon spawning (and dying).

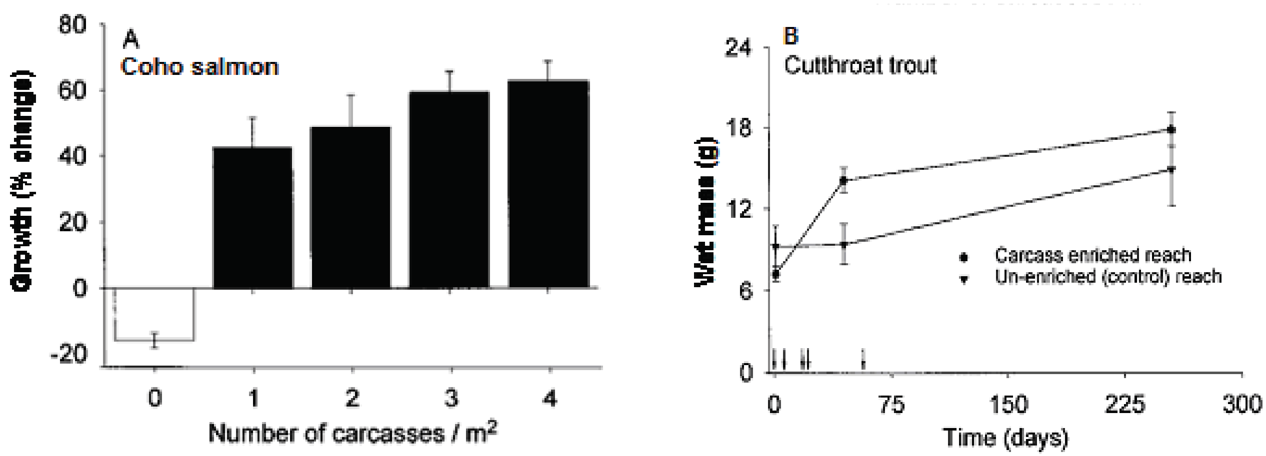
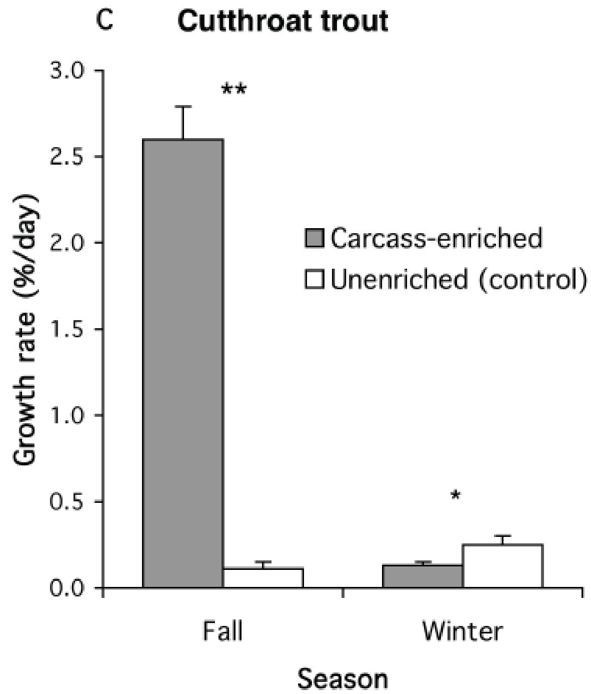


Figure 5—(A) Mean (+ 1 standard error) growth (percent change in wet mass over 66 days) of young coho salmon in artificial streams exposed to 5 salmon carcass treatments. (B) Mean (± 1 standard error) wet mass of cutthroat trout recaptured on 2 dates from stream reaches with (circle, $n = 9$) or without (triangle: control, $n = 5$) experimentally added salmon carcasses. Arrows along the horizontal axis indicate dates when salmon carcasses were added.



(C) Mean (+ 1 standard error) growth rates (% change in wet mass/day) of the cutthroat trout in part (B). Growth rates are calculated between successive capture intervals. Asterisks indicate significant differences in growth rate within a season (*t*-test): *P , 0.05; **P < 0.01. (Redrawn from data in Wipfli et al. (2003), Table 4.)

Questions

1. Does the presence of salmon carcasses affect the growth of fish? Support your answer by referring to specific data in the figures.
2. What are some likely ways that salmon carcasses could affect fish growth—i.e., how could the nutrients from salmon carcasses get to or affect fish growth?
3. Speculate as to why, in the winter, the growth rates of trout in the enriched stream reach were almost the same (actually, a little less than) the growth rates of trout in the unenriched stream section (Figure 5B and 5C).

Part 2—Do Marine-Derived Nutrients Affect Stream Organisms?

Instructions—Second Jigsaw Group

Each person should take a few minutes to explain his/her figure(s) and the major conclusions about it. When everyone understands all the individual figures, the group should use its combined knowledge to answer the questions below and come up with an overall description of the role of salmon in the nutrient cycle of stream ecosystems. (Try making a diagram!)

Questions

1. What are some likely ways that salmon carcasses affect fish growth—i.e., how could the nutrients from salmon carcasses get to or affect fish growth? Support your answer by referring to specific data in the figures.
2. Compare the two methods (observational study and experiment) used to answer these questions. What are the strengths and limitations of each?

Part 3—How Does Marine-Derived Nitrogen Get to Stream-Side Terrestrial Ecosystems?

Instructions

After reading the background information for the figure, work with a small group to first describe and then interpret the data in the figures below. Use the Step 1–Step 2 approach described below to interpret the two figures.

- ***Step 1:*** Describe the graph and what it shows. Make sure you understand how the figure is set up, what the axes show, and what information is depicted. Carefully describe the overall patterns in the data.
- ***Step 2:*** Try to interpret the data. What do they tell you about the effect of salmon on marine-derived nutrient levels in the stream ecosystem?

When you understand the figures, try to answer the questions about the figures. Be prepared to volunteer or be called on during our class discussion to explain a figure or share your answer to a question.

Figures 6, 7, and 8—Background

From: Mathewson, D., M. Hocking, and T. Reimchen. 2003. Nitrogen uptake in riparian plant communities across a sharp ecological boundary of salmon density. *BMC Ecology* 3:4 (Figure 6) and Hocking, M., and T. Reimchen. 2002. Salmon-derived nitrogen in terrestrial invertebrates from coniferous forests of the Pacific Northwest. *BMC Ecology* 2:4 (Figures 7 and 8). Figures used in accordance with BioMed Central Open Access license agreement (**http://www.biomedcentral.com/info/about/license**).

Samples of vegetation and terrestrial macroinvertebrates were collected from two salmon-bearing watersheds, the Claste and Neekas Rivers, in coastal British Columbia. A waterfall, 1 km upstream on the Claste River and 2.1 km upstream on the Neekas River, blocks further upstream salmon migration in both rivers.

Foliar (leaf) samples were collected within 15 m of the river, from 50 m below to 50 m above the waterfall. Species collected were deerfern *(Blechnum spicant)*, false azalea *(Menziesii ferruginea)*, devil's club *(Oplopanax horridus)*, salmonberry *(Rubus spectabilis)*, Alaskan blueberry *(Vaccinium alaskaense)*, red huckleberry *(V. parvifolium)* and western hemlock *(Tsuga heterophylla)*. At least 9 individuals of each species were sampled at each site. Terrestrial macroinvertebrates were collected using pitfall trap arrays and hand collecting along the rivers above and below the falls, up to 100 m from the stream.

Both plant and invertebrate samples were analyzed for stable nitrogen isotopes ($\delta^{15}N$). Invertebrate samples were also analyzed for stable carbon isotopes ($\delta^{13}C$). For both elements, an elevated heavy isotope ratio is indicative of marine-derived nutrients (MDN). The researchers looked at both N and C in the invertebrates to try to figure out whether the animals were getting MDN directly from salmon carcasses or by consuming MDN-enriched plants.

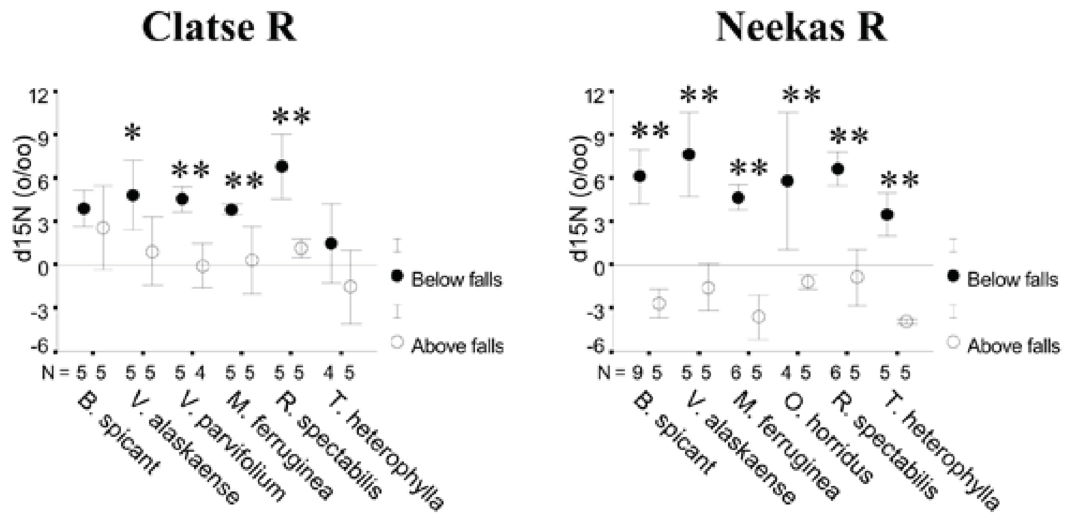


Figure 6—δ15N values in riparian vegetation collected immediately below and above waterfall barriers to salmon at Claste and Neekas Rivers, British Columbia, Canada. *t*-test results: *P < 0.05; **P < 0.01.

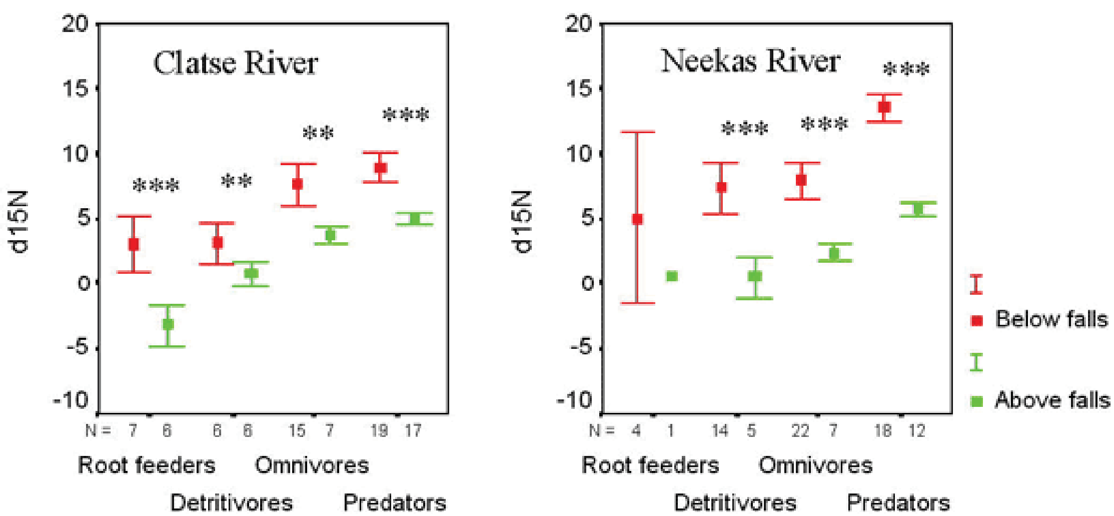


Figure 7—δ15N values in four trophic groupings of litter-based invertebrates collected immediately below and above waterfall barriers to salmon at Claste and Neekas Rivers, British Columbia, Canada. Invertebrates are ranked (left to right) based on increasing consumption of animal protein. *t*-test results: **P < 0.01; ***P < 0.001.

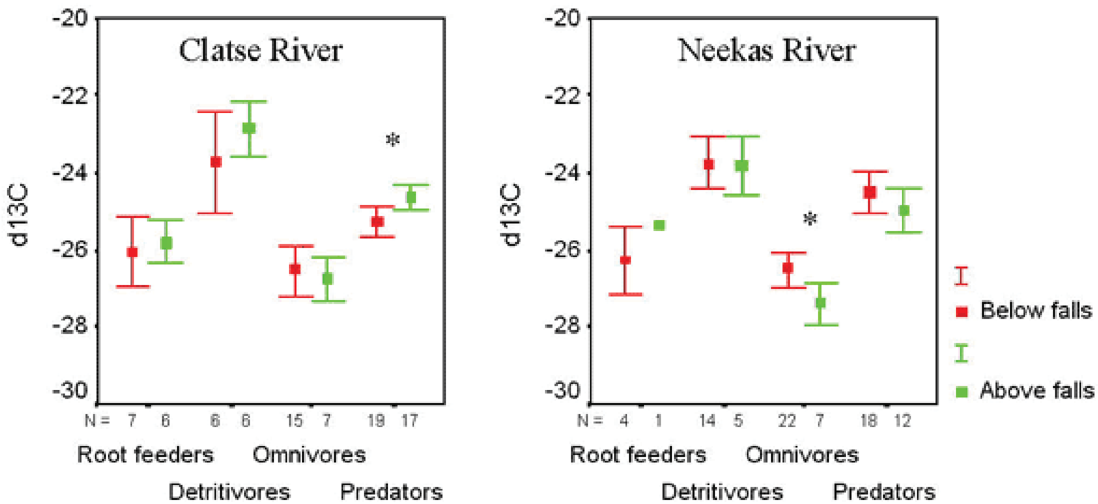


Figure 8—$\delta^{13}C$ values in four trophic groupings of litter-based invertebrates collected immediately below and above waterfall barriers to salmon at Claste and Neekas Rivers, British Columbia, Canada. Invertebrates are ranked (left to right) based on increasing consumption of animal protein. *t*-test results: $^*P < 0.05$.

Questions for Figures 6, 7, and 8

1. Do salmon-delivered (marine-derived) nutrients get into the food web of the riparian community along salmon spawning streams? If so, what nutrients (N or C) and what part or parts of the community (e.g., plants, root feeders, etc.)? Support your answer by referring to specific data in the figures.
2. In the invertebrates, is there a difference between the effects of salmon on $\delta^{15}N$ and $\delta^{13}C$? What does this tell us about how MDN are getting to the invertebrates?

Figure 9—Background

From: Hilderbrand, G.V., T.A. Hanley, C.G. Robbins, and C. Schwartz. 1999. Role of brown bears *(Ursus arctos)* in the flow of marine nitrogen into a terrestrial ecosystem. *Oecologia* 121: 546–550. Panel A originally appeared as Figure 1a, page 548; panel B originally appeared as Figure 2, page 548. Used with permission of the author and Springer Science and Business Media.

Bears consume large quantities of salmon during spawning runs. Some of the nutrients from the consumed salmon, especially nitrogen, will be excreted a short time later in wastes (urine and feces). This study examined the effects of bears on the redistribution of salmon-derived nitrogen into the riparian forest.

Study sites were located on the Kenai Peninsula, Alaska. Mystery Creek had runs of several salmon species and abundant brown bears. Russian River had abundant salmon but few bears (because of the presence of human anglers). Cooper Creek had few salmon or bears.

Spruce needles were collected along 2 transects/site running perpendicular to the stream and analyzed for $\delta^{15}N$ signature. The spatial distribution of bears was measured using position data from radio- or satellite-collar tracking of the movement patterns of 59 female bears. Bear spatial distributions was assumed to be directly proportional to N deposition in wastes (because who is going to measure it directly?).

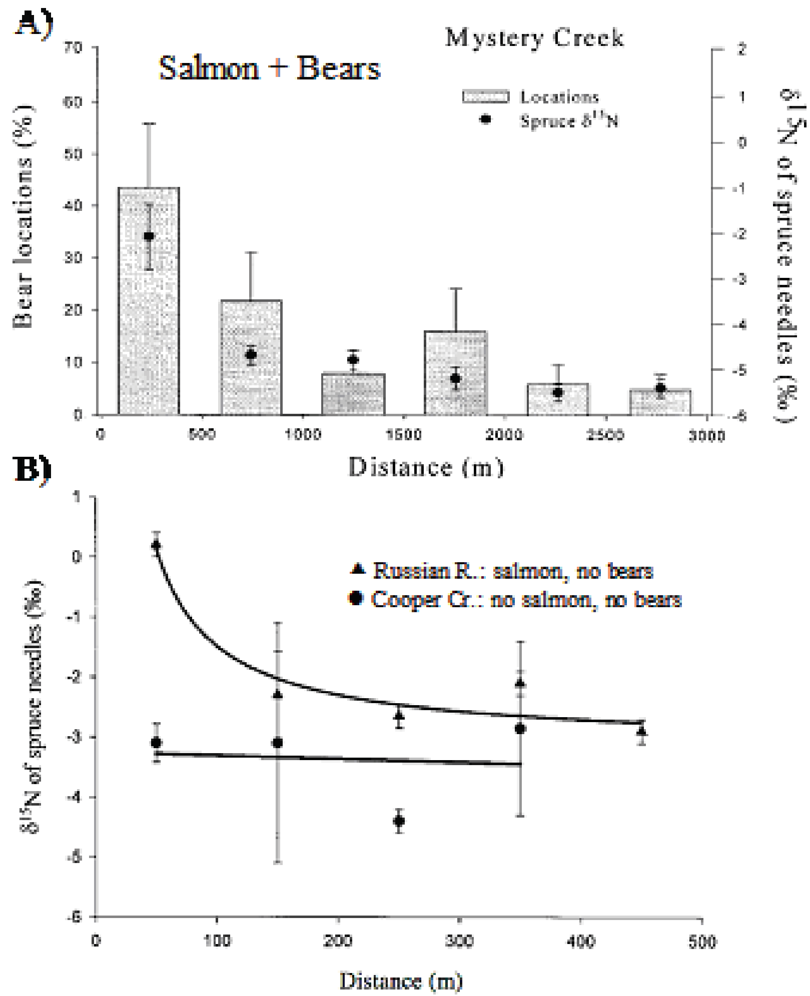


Figure 9—Spatial patterns of adult female brown bear locations (mean ± 1 standard error) (A) and $\delta^{15}N$ signatures of spruce needles (mean ± 1 standard error) (A and B) in relation to distance from a stream. Note the difference in the scale of the horizontal axis (Distance) in the two graphs. Bears were only present at Mystery Creek; salmon were not present at Cooper Creek. No spruce were encountered beyond 400 m from Cooper Creek and 500 m at Russian River.

Questions for Figure 9

1. What effect does salmon spawning have on the level of MDN in riparian plants? Support your answer by referring to specific data in the figures.
2. What effect do bears have on the delivery of MDN to riparian plants—i.e., are bears a significant vector for the movement of MDN into the terrestrial ecosystem? Support your answer by referring to specific data in the figures above.
3. Do the effects of salmon and bears (on MDNs) appear to be independent of one another? Explain.
4. In addition to waste products, what are some other ways that bears might deliver MDN to riparian ecosystems?
5. Other than by bears, make one or two hypotheses about how the MDNs are being transported from the stream to the terrestrial ecosystem. How could you test these hypotheses?

Part 4—Does Salmon-Derived Nitrogen Affect the Terrestrial Ecosystem?

Instructions

After reading the background information for the table and figures, work with your neighbor (or a small group) to first describe and then interpret the data in the figures below. Use the Step 1–Step 2 approach described below.

- *Step 1:* Describe the table as well as the graph and what it shows. Make sure you understand how the figure is set up, what the axes show, and what information is depicted. Carefully describe the overall patterns in the data presented in both the table and the figure.
- *Step 2:* Try to interpret the data. What do they tell you about the effect of salmon on marine-derived nutrient levels in the stream ecosystem?

When you understand the table and the figure, try to answer the questions about them below. Be prepared to volunteer or be called on during our class discussion to explain the data or share your answer to a question.

Table 1 and Figure 10—Background

From: Helfield, J. M., and R. J. Naiman. 2001. Effects of salmon-derived nitrogen on riparian forest growth and implications for stream productivity. *Ecology* 82(9):2403–2409.

Study sites were in the Kadashan and Indian River watersheds on Chichagof Island in SE Alaska. Each watershed contained one spawning and one reference site. Spawning sites were adjacent to reaches of stream where salmon spawned. Reference sites were adjacent to reaches without spawning, either because of a waterfall barrier or being located above the upstream extent of spawning. At each site, samples were taken along four 100-m transects extending laterally from the stream. Vegetation (leaves) of Sitka spruce and understory plants were analyzed for $\delta^{15}N$ and carbon: nitrogen ratio. Basal area growth (increase in the size of the trunk at ground level) of Sitka spruce was determined from tree cores.

Table 1—Mean carbon: nitrogen (C:N) ratios and $\delta^{15}N$ values in the foliage of riparian vegetation at spawning and reference sites. Sample sizes are shown in parentheses.

	C:N ± 1 SE (*n*)		$\delta^{15}N$ ± 1 SE (*n*)	
Species	Reference	Spawning	Reference	Spawning
Sitka spruce (*Picea sitchensis*)	39.21 ± 2.01 (10)	32.73* ± 1.46 (10)	−3.34 ± 0.33 (32)	0.63* ± 0.32 (44)
Devil's club (*Oplopanax horridus*)	17.21 ± 0.46 (11)	15.75* ± 0.57 (11)	−0.91 ± 0.38 (22)	2.24* ± 0.34 (28)
Fern (*Dryopteris dilatata, Athyrium filix-femina*)	19.62 ± 1.01 (10)	16.88* ± 0.86 (10)	−3.05 ± 0.42 (19)	0.62* ± 0.36 (27)
Red alder (*Alnus rubra*)	16.51 ± 0.89 (10)	16.56 ± 1.14 (10)	−1.04 ± 0.09 (10)	−0.91 ± 0.11 (21)

Notes: Dryopteris dilatata and *Athyrium filix-femina* are grouped together because no significant differences in foliar C:N or $\delta^{15}N$ were detected between the two species [$P(t_{44(2)} > 1.85) > 0.05$].

* Significant difference between spawning and reference sites, as determined by two-sample *t* tests ($\alpha = 0.05$).

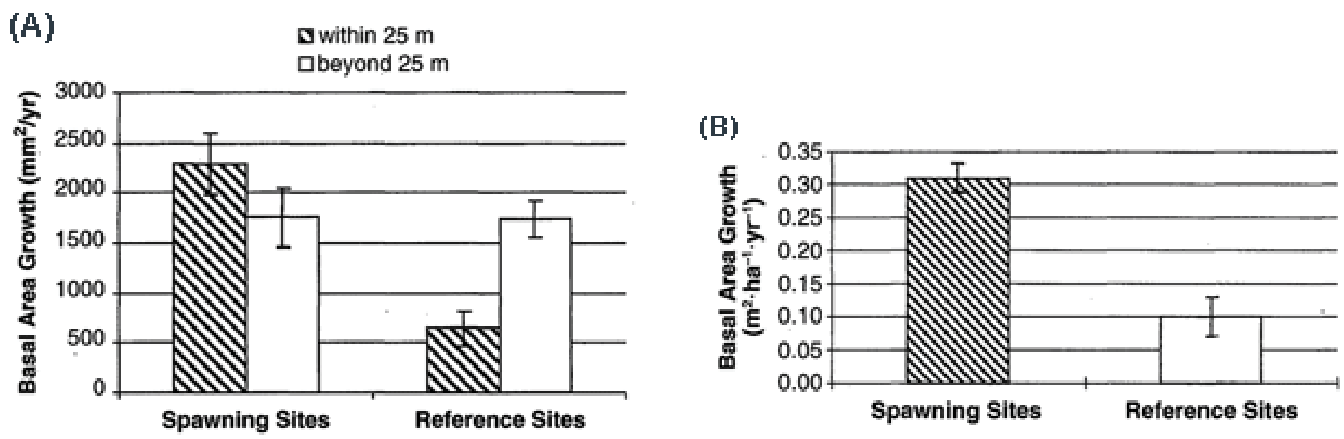


Figure 10—(A) Mean (± 1 standard error) annual basal area growth (mm2/year) of riparian Sitka spruce at spawning and reference sites. Two-factor ANOVA indicates a significant salmon effect (i.e., spawning vs. reference sites, P = 0.01), no significant effect of distance from the stream (i.e., within 25 m vs. beyond 25 m, P = 0.38), and a significant interaction effect of salmon and distance (P = 0.01). (B) Mean (± 1 standard error) annual basal area growth per unit area of riparian Sitka spruce at spawning and reference sites.

Questions

1. What is the significance of the carbon: nitrogen ratio?
2. What effect does salmon spawning have on the nutrient status of riparian plants?
3. Does MDN affect the growth of Sitka spruce?
4. The legend of Figure 10 mentions an interaction between salmon and distance. What is an interaction in this sense, and can you point it out graphically in Figure 10?
5. What is the difference between what is shown in Figure 10-A and what is shown in Figure 10-B?
6. Based on these results, what differences would you expect to find between the riparian forests of areas with salmon spawning and forests without salmon spawning?