

*Running the Numbers*..... 2  
*An Ecological Cornerstone*..... 3  
*Changing the Freshwater Community*..... 4  
*Effects of Predation on Fish*..... 4  
*Sustainability from a Food Web Perspective*... 5  
*A Change of Approach*..... 5

# Science

## FINDINGS

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*"Science affects the way we think together."*

Lewis Thomas

### THE FISH-BASED FOOD WEB: WHEN PREDATOR AND PREY CONNECT



Photo credit: E. H. Armstrong

**A** Bird populations can escalate from a few hundred to tens of thousands during spawning runs. Salmon carcasses often are carried far from the streams to such places as bald eagle nests.

*"'Tis true; there's magic  
in the web of it."*

Othello, William Shakespeare  
1564-1616

**S**cene: Coastal southeastern Alaska during spawning season. Rivers choked with fish. Birds and bears also choked with fish. People staked with cameras.

When the anadromous fish—especially salmon, but also charr, smelt, and others—return to the rivers on their way home to spawn, they attract a lot of attention. Tourists flock to see them, or more specifically, to see the bears feeding on them. Hundreds of bears, that is, and mink and wolves. Thousands of bald eagles and

crowns. Tens of thousands of gulls. Not to mention marine hunters such as whales, sea lions, and otters that chow down around the estuaries. Great photo opportunities. So is this sustainable tourism, or rampant ecology?

"If you look around up here with an ecologist's eyes, you quite rapidly see the megaimportance of fish: all those carcasses in and around the streams, the bears and other critters chewing on them," says Mary Willson. "But almost nobody had explored the consequences of this. It just sat there in the minds of locals." Willson was an ecologist at the PNW Research Station's Forestry Sciences Laboratory in Juneau, Alaska, and had been studying ecological interactions in temperate rain forests.

#### IN SUMMARY

*This issue of "Science Findings" focuses on ecologist Mary Willson's research in Alaska that has revealed anadromous fish to be "cornerstone species." A cornerstone species provides a resource base to support much of an ecosystem. Anadromous fish, in this case, have been found to support much of the Pacific coastal ecosystem. Key findings of Willson's team research are that the productivity of freshwater and riparian ecosystems is fueled by marine-derived nutrient subsidies from anadromous fishes. Many wildlife species depend seasonally on anadromous fish runs. In some cases predator species' reproductive biology is closely tied to the timing of fish runs.*

*Managers' understanding of the basic ecology of riparian areas with anadromous fish runs can help provide ecological sustainability and maintain cascading ecological function. A piecemeal approach is inadequate to address the tight links among fish populations, stream and riparian ecology, wildlife and wildlife habitat. Maintenance of the functional system and its nutrient transfer agents requires broad integrated management techniques.*

According to Willson, cross-habitat exchanges are beginning to be recognized as crucial components of population ecology, components that have played a pervasive role throughout the evolution of many species of fish and wildlife.

"The developing picture is one of critical and reciprocal interactions between aquatic and terrestrial systems. Many wildlife species, both aquatic and terrestrial, depend on fish as a food resource," she says. "It seems so obvious, now, that we can't take each system in isolation." In fact, Willson and her colleagues refer to the fish as a "cornerstone species" because they believe the fish provide a resource base that supports much of the coastal ecosystem.



## KEY FINDINGS



- In Alaska, and formerly all along the Pacific coast, productivity of freshwater and riparian ecosystems is fueled by marine-derived nutrient subsidies from anadromous fishes.
- Many wildlife species depend seasonally on anadromous fish runs; in some cases predator species' reproductive biology is closely tied to the timing of fish runs.
- Anadromous species are cornerstones of a complex food web in coastal ecosystems, in which predators are affected by availability, health, and numbers of prey, and prey are affected by patterns and levels of predation.

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<http://www.fs.fed.us/pnw>

## RUNNING THE NUMBERS

The prodigious size of spawning runs is suggested by commercial harvest figures. In 1985, about 147 million salmon were harvested in Alaska; in 1995, the salmon harvest topped 217 million. Before the late 1800s, the only factors preventing these numbers of fish from actually reaching spawning streams were localized heavy subsistence by indigenous people, or natural disturbances such as landslides or glaciers blocking access to streams.

Despite the huge harvest levels, many fish escape this human hazard. In southeast Alaska, average "escapements" of pink and chum salmon sometimes number over 10,000 fish per stream; runs of several thousand are common. Successful spawning groups of herring and eulachon can number in the hundreds of thousands, and often millions.

On the other side of the equation, over 40 species of mammals and birds in southeast

Alaska forage on salmon in their freshwater habitats; some feed on adult salmon and carcasses, others on eggs and juveniles.

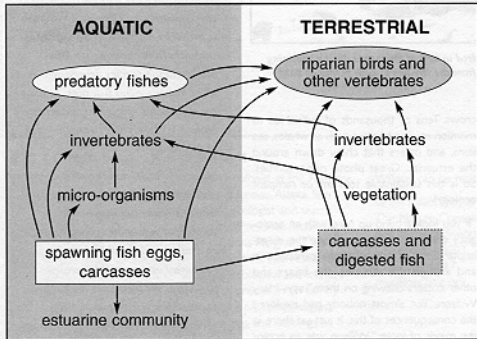
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A complex food web based on anadromous fishes shows the multiple links between the aquatic and terrestrial systems. Marine-derived nutrients pass up through the aquatic food web, and also enter the terrestrial food web. The relative magnitudes of nutrient flow along various pathways have yet to be determined.



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## AN ECOLOGICAL CORNERSTONE

What are the effects, then, of this huge supply of fish on their hungry predators?

"The capture of these fish rewards a predator well," says Willson. "The amount of lipids in a prey item is usually a rough indicator of energy yield to a predator, and their lipid value is considerably higher than that of most other marine fishes commonly eaten by sea birds and sea mammals." She notes that no comprehensive picture of lipid variations is yet available, but the influx of spawning fish, simply measured in terms of numbers, biomass, or energy content, provides a large food resource for consumers.

The sheer numerical magnitude of predators to spawning runs suggests that the availability of spawning fish is crucial. For example, when the eulachon (a smelt) run in spring, the number of gulls present along streams increases rapidly from several dozen to 50,000–100,000, and the number of bald eagles also rises, from just a few to 1,000 or more. It's exploitation, plain and simple, seasonal exploitation. And the ecological importance of it has finally begun to be documented.

Take bears. To prepare for hibernation, bears consume vast amounts of food in late summer and fall, laying down the necessary fat stores by eating as much as 40 pounds of food a day, sometimes more. Bears give birth during hibernation, relying on this fat store to produce milk for their young; it is believed that well-fed, fat, female bears reproduce more successfully than thin ones. As further evidence of the advantages of access to fresh fish, coastal brown bears appear to mature earlier than interior bears.

Likewise, mink benefit from the spawning fish, so much so that they have apparently delayed the timing of their breeding cycle so that lactation—with its high energy cost—occurs when salmon carcasses are available. A study of bald eagles along the Chilkat River in southeast Alaska revealed they were more likely to breed and laid eggs earlier than eagles that lacked access to the fish food source. Those eagles that fledge at the time of spawning may increase their chances of surviving the break from their parents when they can easily acquire food high in energy.

## MANAGEMENT IMPLICATIONS

- Understanding the basic ecology and managing stream and riparian zones in forested areas with anadromous fish runs depends on recognizing the close integration of terrestrial and aquatic ecosystems. They are linked, and the costs and benefits flow both ways.
- Both fish populations and populations and habitats of terrestrial nutrient-transfer agents must be maintained in order to provide ecological sustainability, maintain cascading ecological functions, and continue to provide ecological goods and services.
- A piecemeal approach is inadequate to address the tight links among fish populations, stream and riparian ecology, and wildlife and wildlife habitat.
- Maintenance of the functional system and its nutrient transfer agents requires broadly integrated management.



**A** Bears store up as much body fat as possible before going into hibernation, and can consume more than 40 pounds of food per day. Females will draw on their fat stores while nursing their young.

Migratory birds also vote by the numbers: May sees many thousands of Thayer's gulls pausing during their migration to breeding grounds in the Canadian Arctic to feast on spawning eulachon. Migrating red-breasted mergansers throng the river mouths to harvest the same plentiful food.

And let's not forget the people. Commercial harvest is today's oversized outgrowth of traditional human harvest: settlement patterns of Native Americans along the northwest coast were often determined by

locations of salmon runs, and indigenous people in Alaska and northwestern Canada still move seasonally to traditional fish camps. In fact, Willson notes, this year there were chum salmon flound in to help people in interior Alaska along the Yukon River; "in the old days, they and their sled dogs would just have died if the salmon run failed."

## CHANGING THE FRESHWATER COMMUNITY

**T**he effect of spawning fish runs is not just a matter of sating hunger among predators. The freshwater community reacts from top to bottom once predator meets prey, according to Willson.

After they spawn, most salmon die. That leaves their carcasses in the stream, to catch on logs and rocks, or stay stranded in the shallows. Feeding on the carcasses, a rich community of algae, fungi, and bacteria develops, and populations of invertebrates increase.

"These invertebrates then serve as food for fish in the stream, including juvenile salmon," says Willson. "Fish biologists have established that juvenile salmonids contain more marine-derived nitrogen and grow faster in streams with salmon carcasses than in those without."

But perhaps more startling in their extent are the potential fertilizer effects. Living and dead salmon are commonly hauled by predators such as bears onto stream banks, then tens of feet back into the forest. Eagles also move salmon to the streamside, and ravens and crows stash bits of salmon in trees and under grass and rocks.

## EFFECTS OF PREDATION ON FISH

**T**hese spawning fish clearly affect the lives of their predators, but what of the reciprocal relation? Do predators affect fish?

"The evolutionary ecology of the life-history of anadromous fishes is still largely speculative, but these patterns are of both academic and management interest, and need to be better understood," Willson says. "Predation, in general, is seldom random, and predation on anadromous fish is no exception." She notes that tradeoffs for predators between foraging benefits and predation risks are thought to affect their patterns of habitat use.

Life history theory suggests that semelparity—reproducing only once in a lifetime, as most Pacific salmon do—evolves when the probability of surviving to reproduce again is low. Predation certainly contributes to the low odds, as do the costs of extensive migration and intense sexual competition.

It is possible to track by isotopic markers the marine-derived nutrients passing from salmon bodies into soil and then to riparian vegetation. "The nutrients passed to the terrestrial system probably pass up the food chain and may affect not only vegetation but also animal consumers," says Willson. "Our preliminary results suggest that bird populations are denser on streams with salmon runs. And we think that riparian vegetation fertilized by fish probably does grow faster."

The magnitude of nutrient input from salmon differs from tiny to tremendous, according to Willson. The example of phosphorus, which is often limited in nutrient-poor freshwater systems, helps illustrate the case.

In Lake Iliamna in western Alaska, a good run of 24 million sockeye salmon adds 170 tons of phosphorus to the lake per year; a poor run of less than half a million adds less than 7 tons. Figures from the Karluk Lake system in south-central Alaska show 1 million sockeye and 4 million pink salmon added 27 tons of phosphorus to the annual nutrient budget of the lake system. Willson points out that this is equiv-

alent to about 0.025 ounce of phosphorus per square foot of lake surface, which is equal to the recommended application of a standard commercial fertilizer to evergreens and other trees!

Other calculations suggest, allowing for average levels of predation and salmon runs, that phosphorus will be added to the terrestrial nutrient cycle at a rate of 6.7 pounds per acre. "In some cases, the input of phosphorus from anadromous fishes overwhelms that from other sources," says Willson. "In other cases, the input may be modest but nevertheless have a large effect on productivity in nutrient-poor systems."

Import of biomass and nutrients derived from the sea—nitrogen, phosphorus, carbon, and micronutrients—to fresh water and to land significantly enhance the productivity of freshwater systems. "When you consider that most of forested lands in southeast Alaska is within 0.6 mile of anadromous fish streams, you see that the effect of marine-derived nutrients is pervasive," Willson adds.

But as with many aspects of cross-habitat exchange, assessment of this fertilizer effect is only just beginning.

Freshwater predation also has the potential to change the duration and intensity of sexual selection, according to Willson. For example, successful predation shortens in-stream life and thus the period of intrasexual competition and nest defense. Further, males develop hooked, toothy jaws and dorsal humps as part of sexual selection. Conspicuous dorsal humps could make them more vulnerable to bear predation in shallow streams; in some cases, predation seems to be sex-specific, further altering sex ratios and patterns of sexual selection.

The anadromous phenomenon and its associated predator-prey interactions is pervasive. Particularly in the Northern Hemisphere, wherever there are or used to be anadromous fishes, the reciprocal effects of their spawning runs tend to penetrate far inland, for example, up the Yukon and Columbia Rivers, Willson says. Even where the spawning runs have no marine compo-

nent, it is likely that such freshwater species as shad or suckers have similar relations with aquatic and terrestrial systems.

In the light of depleted salmon runs in regions south of Alaska, the question becomes: What happens to this relation when the supply of fish is no longer so plentiful?

## SUSTAINABILITY FROM A FOOD WEB PERSPECTIVE

The immediate answer is simple: we don't know yet. "When we routinely harvest as much as 80 or 90 percent of a run, logic tells us it has to have some effect on all those predators," Willson points out. "But we do not yet know many of the simple answers: What happens to bears and wolves when a run is lost? Do they move to the next watershed, where the fish are still running? Do they just get thin? What does this mean for their reproductive cycle?"

And what does it mean for all the other critters and the vegetation that have evolved to make use of marine nutrients courtesy of the annual salmon run?

If the answers are not yet in, the question does strongly suggest we reassess our current concepts of sustainability. The simplistic commercial harvest perspective involving "escapement" may need to be turned on its ecological head.

### A CHANGE OF APPROACH

What cross-habitat studies require is broader and more synthetic thinking than individual disciplines are used to, and that's possibly what has gotten in the way. It requires looking at things extensively rather than only intensively," Willson says.

She acknowledges that much work has yet to be done to quantify preliminary studies, from documenting the fertilizer effects, to observing adjustments of those mammals that lose their local salmon runs, and tracking the nutrient exchange through isotopic markers in vegetation, insects, and birds.

"A change of perspective—to actively include the wildlife participants in the interaction—is long overdue. Interactions among species are a central component of ecosystem function and, hence, of maintaining biodiversity in ecological systems," Willson points out.

The time has come, perhaps, to recognize the cornerstone nature of anadromous fish populations, their status with their predators as ecosystem engineers, and to incor-

"To define sustainability from a natural resource perspective, we need studies that show first how many salmon it takes to support a certain level of wildlife—the bears, otters, wolves, eagles, dippers, even squirrels and deer," says Willson. "Then we need a margin in case the berry crop fails and that food source is gone, then enough extra to allow for the pickiness of female salmon in choosing partners and nesting sites."

Then, maybe, we can talk about what's sustainable in terms of a commercial harvest. "Escapement," as she points out, is an anthropomorphic term that does not comprehend the fish-based food web so fondly anticipated by tourists in Alaska, and has left a legacy around many ocean margins of the world.

"Escapements sufficient to maintain a fishery in a management district may be inadequate from a wildlife perspective," she explains. "The fish populations of small

streams are not entirely substitutable resources for many species of wildlife, although they may be for commercial fishers." In addition, commercial harvests are commonly harvests of mixed stocks of fish, thus automatically affecting salmon runs on a regional rather than a local scale.

So in the Pacific Northwest, where so many salmon runs are under siege, what are the implications? Willson believes that collapse of regional spawning runs seriously limits options for wildlife consumers. Long-distance emigrations, impaired reproductive success, and increased mortality become more probable.

Any such undermining of a species makes it more vulnerable to other events, ranging from earthquakes and landslides to megaharvests, climate change, and oceanic cycles, according to Willson. Hatchery stocks also can wreak greater havoc on weakened stocks.

*"Rivers are linear systems which serve to evacuate water falling on the continental masses towards the oceans."*

Recognizing our changing viewpoints: from *River Fisheries*, FAO Fisheries Tech. Pap. 262, 1985

porate this understanding into ecosystem-based plans for land management, fishery harvest, and conservation.

In other words, to substantiate the hypotheses long supported by throngs of tourists and photographers, and untold herds of hungry wildlife.

### FOR FURTHER READING

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### WRITER'S PROFILE

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