

Pacific salmon and the ecology of coastal ecosystems

Daniel E Schindler¹, Mark D Scheuerell², Jonathan W Moore¹, Scott M Gende³, Tessa B Francis¹, and Wendy J Palen¹

One of the most spectacular phenomena in nature is the annual return of millions of salmon to spawn in their natal streams and lakes along the Pacific coast of North America. The salmon die after spawning, and the nutrients and energy in their bodies, derived almost entirely from marine sources, are deposited in the freshwater ecosystems. This represents a vital input to the ecosystems used as spawning grounds. Salmon-derived nutrients make up a substantial fraction of the plants and animals in aquatic and terrestrial habitats associated with healthy salmon populations. The decline of salmon numbers throughout much of their southern range in North America has prompted concern that the elimination of this “conveyor belt” of nutrients and energy may fundamentally change the productivity of these coastal freshwater and terrestrial ecosystems, and consequently their ability to support wildlife, including salmon. If progress is to be made towards understanding and conserving the connection between migratory salmon and coastal ecosystems, scientists and decision-makers must explore and understand the vast temporal and spatial scales that characterize this relationship.

Front Ecol Environ 2003; 1(1): 31–37

A major advance in ecology has been the realization that communities are not passive collections of organisms that simply reflect the geophysical template of ecosystems. Instead, animals regulate the flows of energy and nutrients in ecosystems through their consumption and digestion as well as through their behaviors and death. Animals also indirectly control these flows by regulating the population dynamics of other organisms with which they interact, for instance as predator and prey.

Pacific salmon (*Oncorhynchus spp.*) provide one of the most impressive examples of animals controlling the flow

of nutrients and energy through ecosystems. Five species of North American salmon and two eastern Asian species are semelparous (reaching sexual maturity, spawning once, and then dying) and anadromous (spawning in freshwater streams, rivers, and lakes after reaching maturity in the northern Pacific Ocean). This life history strategy results in a steady flow of energy and nutrients from the broad expanse of the ocean to confined freshwater ecosystems, where salmon carcasses, gametes (mature eggs and sperm), and metabolic waste are ultimately deposited. Because salmon are rich in nutrients and energy, are relatively large fish (weighing 2–20 kg, and occasionally over 50 kg, at maturity), and can achieve exceptionally high densities in freshwater ecosystems, this “conveyor belt” acts as a major source of nutrients and organic energy to coastal freshwater ecosystems (Gresh *et al.* 2000; Figure 1).

Ecologists have recognized the importance of this influx since the 1930s (Juday *et al.* 1932). Nevertheless, we are only now beginning to understand its role in the productivity of freshwater and riparian habitats, and the population dynamics of organisms that live in recipient ecosystems (Cederholm *et al.* 1999; Willson *et al.* 1998; Gende *et al.* 2002; Naiman *et al.* 2002). Here we provide an overview of the state of knowledge concerning the roles of Pacific salmon in the ecology of coastal ecosystems, and discuss this in relation to the management of the coastal resources of western North America. Wild salmon populations have been reduced greatly throughout much of their North American range over the last century, due to fisheries exploitation, habitat loss, and hatchery practices (NRC 1996; Gresh *et al.* 2000). These losses may represent a serious impediment to maintaining productive and

In a nutshell:

- Certain salmon species return to streams and lakes to spawn and die
- The ocean-derived nutrients and energy contained in their bodies are deposited in the surrounding freshwater and terrestrial ecosystems.
- Recent declines in salmon numbers due to fisheries exploitation, habitat loss, and hatchery practices may be putting this vital process at risk
- Such losses may inhibit the productivity of these freshwater ecosystems, limiting their ability to support wildlife, including salmon
- Long-term, ecosystem-scale studies are needed to understand the implications for fishery management and ecosystem resilience in the face of environmental change

¹ Department of Zoology, University of Washington, Box 351800, Seattle, WA 98195-1800 (contact author: deschind@u.washington.edu); ² School of Aquatic and Fishery Sciences, University of Washington, Box 355020, Seattle, WA 98195; ³ Pacific Northwest Research Station, 2770 Sherwood Lane, Suite 2A, Juneau, AK 99801



Figure 1. Sexually mature sockeye salmon migrating into a small stream to spawn in the Bristol Bay region of southwest Alaska.

diverse coastal ecosystems and to the future existence of the salmon populations (Figure 2).

■ Connecting lakes and streams to the ocean

Salmon accumulate over 95% of their biomass in the ocean, setting the stage for a substantial shift of energy and nutrients when they return to their natal habitats to spawn (Groot and Margolis 1991; Cederholm *et al.* 1999; Gresh *et al.* 2000; Naiman *et al.* 2002). Nutrients from salmon gametes and carcasses are incorporated into freshwater biota, through both the direct consumption of the gametes and body tissues and the uptake of nutrients from decomposing carcasses by bacteria and primary producers, which stimulates the proliferation of benthic algae and invertebrates (Kline *et al.* 1990; Wipfli *et al.* 1998). Similar positive effects have been shown for phytoplankton and zooplankton in the nursery lakes of sockeye

acids. The growth rates of both resident fish and juvenile salmon are particularly improved following the consumption of salmon tissues (Bilby *et al.* 1998). Taken together, these studies of the individual components of the freshwater food web suggest that the presence of anadromous salmon may increase the total productivity of freshwater ecosystems (Figure 3). Evidence from the study of a small estuary suggests that similar processes may be important in confined coastal regions with dense salmon populations (Fujiwara and Highsmith 1997).

Analyses of stable isotope chemistry from plant and animal tissues allow an estimation of how far salmon resources are distributed throughout aquatic and terrestrial food webs (Kline *et al.* 1990; Ben-David *et al.* 1998; Helfield and Naiman 2001; Schindler and Lubetkin 2003). Salmon provide an enriched source of the heavier stable isotopes of C (^{13}C) and N (^{15}N) relative to most other sources in freshwater and terrestrial systems. These natural isotopes provide a way to establish the fate of salmon-derived nutrients. In particular, the proportion of ^{15}N present has been used to quantify the proportion of N derived from salmon as a part of the total nutrient budgets of freshwater plants and animals.

Nearly every trophic level in aquatic ecosystems with dense salmon populations has shown elevated marine N when compared to ecosystems without salmon, or those upstream from a barrier to fish migration (Kline *et al.* 1990; Kline *et al.* 1993; Bilby *et al.* 1996). In some cases, 30–75% of the N in fish and aquatic invertebrates is of marine origin, indicating a strong link to salmon (Naiman *et al.* 2002).

The P and N deposited in fresh



Figure 2. Population of sockeye salmon spawning in a typical stream in southwest Alaska. Carcasses of fish that have already spawned and died are seen in the foreground.



Figure 3. Sculpins are one of many aquatic predators that consume salmon eggs and tissue from carcasses, a foraging strategy that results in a direct and efficient transfer of large quantities of high-quality nutrients. This sculpin, in a river in southwest Alaska, apparently died while attempting to swallow the sockeye salmon egg seen in its mouth.

waters by spawning salmon have been hypothesized to enhance juvenile salmon growth and survivorship by stimulating primary and secondary production in lakes and streams (Juday *et al.* 1932; Kline *et al.* 1993; Wipfli *et al.* 1998). This suggests that declining numbers of spawning adult salmon contribute less marine-derived nutrients to freshwater systems, leading to reduced survival of juvenile salmon. Researchers typically describe this as a positive feedback loop (Bilby *et al.* 1996; Wipfli *et al.* 1998), but the connection has rarely been demonstrated (Naiman *et al.* 2002). Nevertheless, recent work has proposed the setting of management goals, based on the assumption of positive feedback between current and future salmon populations (Schmidt *et al.* 1998; Bilby *et al.* 2001). While the influx of salmon-derived nutrients increases primary and secondary production in some lakes and streams (cf Kyle 1996), in other cases this input is only a small part of the overall nutrient budget of the nursery system (Gross *et al.* 1998).

Caution should be exercised when using stable isotopes to demonstrate a direct relationship between nutrients from salmon and the survival of their offspring. Stable isotopes provide evidence of trophic interactions integrated over time, and isotopic signatures reflect both an individual's position in the food web and the sources of nutrients to the ecosystem (Vander Zanden and Rasmussen 1999). Furthermore, microbial processing of N can raise the proportion of ^{15}N , and therefore isotopic evidence from juvenile salmon enriched in N may provide potentially misleading estimates of the importance of salmon (Gende *et al.* 2002). These problems will be clarified through detailed studies relating the diets, growth rates, and survival rates of organisms that consume salmon resources, coupled with large-scale experiments that manipulate salmon densities.

■ Salmon as ecosystem engineers

Anadromous salmon not only transport nutrients and organic energy from marine to freshwater ecosystems, but also represent a source of mechanical energy in habitats used for spawning. Salmon excavate redds (nests) 10–35 cm deep and 1.1–18 m² in area, depending on species and body size (Groot and Margolis 1991), into which they deposit their eggs. Redd digging alters the composition of sediments and is an intense and predictable source of disturbance to benthic communities in spawning regions of lakes and streams (Figure 4).

During nest digging, salmon act as ecosystem engineers, physically altering the shape and composition of stream and lake beds. For example, digging disturbs the substrate topography, forming substantial ridges and depressions that can change water-flow patterns (Burner 1951) and, over time, may promote stream channel migration. Nest digging also decreases local silt levels (Kondolf *et al.* 1993), and probably increases silt export from spawning streams by creating a suspension of small particles.

Redd digging generally decreases the abundance of periphyton (attached algae) by scouring or burying surface substrata during spawning (Peterson and Foote 2000; J Moore pers obs). It also dislodges benthic invertebrates, increasing drift rates by up to four times and making them susceptible to predation by drift-feeding fish (Peterson and Foote 2000). Benthic insect densities decrease by up to 84% after spawning (Peterson and Foote 2000; J Moore pers obs). It is likely, therefore, that the disturbance associated with salmon spawning may be important in the organization of lake and stream benthic communities.

Disturbance due to nest digging may also influence future salmon survival. For example, spawning decreases substrate mobility by sorting substrata and suspending fine sediments, thereby theoretically reducing shear stress on stream beds. This may lower the risk of incubating eggs



Figure 4. A female sockeye salmon excavating a redd (nest) in southwest Alaska. This digging promotes water flow through the gravel in the streambed and increases the export of fine particles from the stream.



Figure 5. A coastal brown bear consuming a pink salmon along a stream in southeast Alaska. Unconsumed pieces of salmon, seen in the foreground, are often scavenged by smaller consumers, unable to catch live salmon themselves.

and young fish being dislodged and killed during floods (Montgomery *et al.* 1996). In addition, the removal of fine sediments increases interstitial water and oxygen flow, potentially increasing egg survival during incubation. It is therefore possible that the recovery of small salmon populations may be impeded by the poor egg-incubating conditions that develop in the absence of dense populations.

Our understanding of the roles of salmon in freshwater ecosystems is somewhat limited, because it derives mostly from studies focused on single locations over short time scales, often less than 5 years (Kline *et al.* 1990; Kline *et al.* 1993; Bilby *et al.* 1996; Wipfli *et al.* 1998). Salmon do not necessarily show much influence on ecosystems when studied on limited temporal and spatial scales. Variation in salmon populations is characterized by time scale of decades and longer, and appears to be coordinated across areas as large as the northern Pacific Ocean (Mantua *et al.* 1997). In order to gain a complete understanding of the interaction between salmon and freshwater ecosystems, we need to demonstrate that short-term changes in productivity, growth rates, or densities actually translate into longer-term ecological responses at population and ecosystem levels. Also, while stable isotope analyses have shown us the degree to which salmon resources can permeate aquatic food webs, they tell us very little about their effects on the population and community dynamics of the recipient ecosystems (Naiman *et al.* 2002).

■ Fish out of water

Salmon-derived nutrients can be incorporated into terrestrial ecosystems in a number of ways:

- (1) Salmon are consumed by terrestrial predators
- (2) Salmon are dragged from streams, partially consumed, and passed through the digestive systems of birds or mammalian predators and scavengers, such as bears (Ben-David *et al.* 1998; Hilderbrand *et al.* 1999; Reimchen 2000)
- (3) Floods deposit salmon carcasses in the floodplain of spawning streams (Cederholm *et al.* 1989)
- (4) Subsurface water flows transport nutrients into riparian zones (Clinton *et al.* 2002)
- (5) Flying aquatic insects from salmon streams and lakes disperse into riparian forests (TB Francis pers obs)

The relative importance of each of these transport mechanisms varies geographically, with stream size and complexity, and with salmon density (Gende *et al.* 2002).

Terrestrial organisms at nearly every trophic level use salmon-derived nutrients when they are available (Bilby *et al.* 1996; Ben-David *et al.* 1998; Cederholm *et al.* 1999; Gende and Willson 2001; Helfield and Naiman 2001). The pathways by which organisms use salmon-derived nutrients include the direct consumption of salmon tissue by predators or scavengers, the uptake of dissolved nutrients by riparian vegetation, and trophic transfers through food webs. These pathways of nutrient transport and transformation are often connected. For example, bears often kill a large percentage (sometimes over 50%) of small salmon populations (Shuman 1950; Quinn and Kinnison 1999; Reimchen 2000), and carry partially consumed carcasses into riparian forests (Gende *et al.* 2001; Figure 5). Salmon carcasses may then be consumed by a variety of vertebrate scavengers, such as mink, marten, or birds, and/or colonized by terrestrial invertebrates (Figure 6). Nutrients leach into soils via invertebrate excretion and microbial decomposition, where they are taken up by streamside vegetation (Bilby *et al.* 1996; Ben-David *et al.* 1998; Helfield and Naiman 2001), or the salmon nutrients may pass up the food chain in the form of invertebrate biomass when insectivorous species, such as parasitic wasps or birds, consume the invertebrates (Gende and Willson 2001).

Despite widespread use at nearly every trophic level, it is unclear whether salmon-derived nutrients elevate biodiversity and the primary and secondary production of terrestrial systems. Sitka spruce in southeast Alaska grow faster along salmon-bearing reaches of streams as compared to stretches without salmon (Helfield and Naiman 2001). However, we do not know whether habitats that are good for salmon are also good for tree growth, or whether salmon-derived nutrients actually stimulate the growth of riparian trees. In fact, the correlation between tree growth rates and the N isotopic enrichment of vegetation suggests that tree growth is at least partially dependent on healthy salmon populations (Helfield and Naiman 2001).

If salmon disappear from a watershed, how do wildlife

populations and terrestrial ecosystems respond? There is some evidence that the population dynamics of some consumers are linked to the availability of salmon, but the magnitude and the mechanisms driving these effects are poorly understood. For example, brown bears occur at population densities 80 times higher in coastal areas than in interior regions inaccessible to salmon (Hilderbrand *et al.* 1999). Within a watershed, a few salmon carcasses may temporarily increase the number of terrestrial invertebrates (such as bottle flies) during the spawning season, but on an annual basis, the number of flies may in fact be more limited by temperature extremes.

The productivity of certain consumers may be strongly affected, or even limited by, the availability of salmon carcasses.

For example, American dippers feed on salmon eggs and young (Obermeyer *et al.* 1999). If the dippers' reproductive success is food-limited, and if salmon provide more food in times of scarcity, then the birds' population dynamics may be driven by salmon density. The relationship will not increase linearly, however; perhaps only a few salmon are needed per km of stream to satiate dippers, and past this threshold other factors, such as predation or the availability of nest sites, may limit dipper nesting success. To understand the importance of salmon to terrestrial ecosystems, it will be critical to determine the role of salmon-derived resources in limiting the productivity and diversity of riparian habitats and the life histories of the organisms that inhabit them.

■ Salmon in space and time

The great diversity of morphological and life history characteristics among Pacific salmon species is mirrored by their successful colonization of an impressive variety of freshwater habitats (Groot and Margolis 1991). Salmon spawn prolifically in streams less than 1 m wide and ponds less than 1 m deep, as well as in some of the largest rivers and lakes in the world, and show substantial morphological and life history adaptations to these disparate habitats (Taylor 1991; Quinn *et al.* 2001). Variation in attributes such as body size, fecundity, and the amount of time spent in fresh versus salt water is the result of both natural and sexual selection (Taylor 1991). Although salmon have successfully colonized many habitats, they are not numerous everywhere. Differences in the productivity and the amount of suitable spawning and nursery habitats in different ecosystems have produced enormous variation in the natural densities of salmon in freshwaters (Groot and Margolis 1991), with over 10 fish per m² in spawning grounds in some areas and relatively few in others. Thus, the importance of salmon-derived nutrients



Figure 6. A spawned-out sockeye salmon, dead for only a few hours, is colonized by flies. Gulls have already scavenged the eyeballs.

and energy to local ecosystems seems to vary widely between locations, depending on the natural capacity of different ecosystems to support salmon populations.

Pacific salmon populations also vary substantially over time. The development of commercial fisheries in the 19th century, often combined with river impoundment and habitat degradation, has greatly reduced salmon densities on spawning grounds throughout the Pacific coast of North America (Gresh *et al.* 2000; Finney *et al.* 2000). These anthropogenic effects are superimposed on the natural temporal variations which regulate salmon populations throughout their range. Much of this natural variation appears to be related to the decade-scale fluctuations in ocean-atmosphere coupling that control the growth and survival rates of juvenile salmon during the marine phase of their life (Mantua *et al.* 1997; Hare *et al.* 1999). Recent paleolimnological studies of Alaskan sockeye populations have shown that temporal variation on 1000-year time scales have also been prominent during the last 2200 years (Finney *et al.* 2002). Salmon populations are responsive to subtle changes in ocean conditions, caused by climatic variations (Mantua *et al.* 1997). Thus, salmon amplify the oceanic climate signal when they deposit marine-derived nutrients in relatively confined freshwater habitats during spawning.

Salmon populations are generally managed over broad spatial scales that encompass identifiable groups of sub-populations, made up of many smaller component populations. The diversity of life history characteristics within these complexes makes salmon stocks, as well as the marine-derived nutrients they supply to coastal ecosystems, more stable over time. An excellent example of this comes from Bristol Bay, Alaska, a region with nearly pristine freshwater habitats and the largest commercial salmon fishery in the world. In this region, the entire sockeye salmon stock has demonstrated more temporal stability than any of its component populations have dur-

ing the last century, despite wide-scale climatic shifts and substantial fishing pressure. In 2002, for example, the total sockeye run to the Naknek/Kvichak River fishing district was only about 4 million fish, or approximately 30% of the long-term average run since 1960. By comparison, that same year, the entire sockeye run to Bristol Bay was about 17 million fish, or about 60% of the long-term average since 1960. Relatively strong runs in other component populations, such as those from the Nushagak and Egegik fishing districts, compensated for the disastrous decrease in returns to the Naknek/Kvichak district.

This greater stability of the total stock complex appears to be the result of compensation among the various locally adapted component populations, which have responded differently to changes in climatic conditions (Hilborn *et al.* unpublished). Thus, over broad spatial scales, the influx of salmon-derived nutrients and energy to coastal ecosystems depends on the total amount of component populations that return to specific freshwater habitats. To maintain resilience in this nutrient conveyor belt, it will be necessary to maintain the integrity of these networks of component populations. Specifically, it is critical not only to preserve freshwater habitats that currently support vigorous salmon populations, but also to protect habitats that have the potential to be productive in the future. It is unclear whether the life history and genetic diversity lost from the salmon systems in the Pacific Northwest (NRC 1996) has already compromised their general resilience to environmental change.

■ Future prospects

More than half a century of ecological and natural history observations have established that spawning populations of Pacific salmon provide energy and nutrients to a remarkable variety of organisms in freshwater and terrestrial ecosystems. The recent flurry of research activity is improving our understanding of the importance of salmon-derived resources for individual ecosystem components, and some of the ecological, hydrological, and biogeochemical processes that control the distribution and use of these nutrients and energy. Nevertheless, there is disagreement regarding the importance of salmon-derived resources to the ecology of coastal ecosystems, and to the maintenance of healthy salmon populations. More small-scale or comparative studies will probably be of limited use in settling this debate.

A major challenge for ecologists will be to resolve the dynamic aspects of the dependence of aquatic and terrestrial ecosystems on salmon at ecologically relevant temporal and spatial scales. It is unlikely that all ecosystem components and organisms respond equally to variation in salmon populations. We need to focus on the thresholds and non-linear components of ecosystem responses to changes in salmon populations, in ways that are relevant to conservation and management. Projects that rely on short funding cycles and limited levels of institutional support

will probably fall short of their intended goals – of understanding the ecosystem-scale implications of salmon-derived resources in aquatic ecosystems. To gain this knowledge we will have to rely on ecosystem-scale experiments (Schindler 1998; Schindler *et al.* 2000), which can be sustained long enough to allow variables with long turnover times (such as soil nutrients and vertebrate populations) to respond. Commercial fisheries have reduced wild salmon populations throughout much of their range over the last century, and therefore can be viewed as a large, sustained manipulation. However, without proper reference systems for comparison, the effects of this manipulation on ecosystem dynamics will be difficult to interpret.

Paleolimnology has provided some information about the responses of lakes, rivers, and streams to long-term changes in salmon populations (Finney *et al.* 2000), but this will be of limited help in understanding riparian and wildlife responses to changes in salmon-derived nutrient subsidies. Adaptive management seems a reasonable approach for establishing experiments of the scale required, but fishery management will need to move beyond its focus on harvest rates if it is to succeed. The challenge for the management and conservation of coastal resources, will be to protect entire networks of productive and viable freshwater habitats. This will help maintain the diversity of salmon populations and life history characteristics that provide system-scale resilience to environmental change.

■ Acknowledgments

We thank Tom Quinn, Ray Hilborn, Don Rogers, Laura Payne, Nate Mantua, Bob Francis, Bob Naiman, Krista Bartz, Jim Helfield, and Jim Edmundson. We also thank the National Science Foundation (Biological Oceanography and LTREB programs) and the Bristol Bay salmon processors for financial support.

■ References

- Ben-David M, Hanley TA, and Schell DM. 1998. Fertilization of terrestrial vegetation by spawning Pacific salmon: the role of flooding and predator activity. *Oikos* **83**: 47–55.
- Bilby RE, Fransen BR, and Bisson PA. 1996. Incorporation of nitrogen and carbon from spawning coho salmon into the trophic system of streams: evidence from stable isotopes. *Can J Fish Aquat Sci* **53**: 164–73.
- Bilby RE, Fransen BR, Bisson PA, and Walter JK. 1998. Response of juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead (*Oncorhynchus mykiss*) to the addition of salmon carcasses to two streams in southwestern Washington, USA. *Can J Fish Aquat Sci* **55**: 1909–18.
- Bilby RE, Fransen BR, Walter JK, and Scarlett WJ. 2001. Preliminary evaluation of the use of nitrogen stable isotope ratios to establish escapement levels for Pacific salmon. *Fisheries* **26**: 6–14.
- Burner, CJ. 1951. Characteristics of spawning nests of Columbia river salmon. *US Fish Wild S Fish B* **52**: 96–110.
- Cederholm CJ, Houston DB, Cole DL, and Scarlett WJ. 1989. Fate of coho salmon (*Oncorhynchus kisutch*) carcasses in spawning streams. *Can J Fish Aquat Sci* **46**: 1347–55.
- Cederholm CJ, Kunze MD, Murota T, and Sibatani A. 1999.

- Pacific salmon carcasses: essential contributions of nutrients and energy for aquatic and terrestrial ecosystems. *Fisheries* **24**: 6–15.
- Clinton SM, Edwards RT, and Naiman RJ. 2002. Forest-river interactions: influence of hyporheic dissolved organic carbon concentrations in a floodplain terrace. *J Am Water Resour Assoc* **38**: 619–31.
- Cummins KW and Wuycheck JC. 1971. Caloric equivalents for investigations in ecological energetics. *Verh Int Ver Limnol* **18**: 1–158.
- Finney BP, Gregory-Eaves I, Sweetman J, *et al.* 2000. Impacts of climatic change and fishing on Pacific salmon abundance over the past 300 years. *Science* **290**: 795–99.
- Finney BP, Gregory-Eaves I, Douglas MSV, and Smol JP. 2002. Fisheries productivity in the northeastern Pacific Ocean over the last 2,200 years. *Nature* **416**: 729–33.
- Footo CJ and Brown GS. 1998. Ecological relationship between freshwater sculpins (*genus Cottus*) and beach-spawning sockeye salmon (*Oncorhynchus nerka*) in Iliamna Lake, Alaska. *Can J Fish Aquat Sci* **55**: 1524–33.
- Fujiwara M and Highsmith RC. 1997. Harpacticoid copepods: potential link between inbound adult salmon and outbound juvenile salmon. *Mar Ecol-Prog Ser* **158**: 205–16.
- Gende SM and Willson MF. 2001. Paserine densities in riparian forests of southeast Alaska: potential role of anadromous spawning salmon. *Condor* **103**: 624–29.
- Gende SM, Quinn TP, and Willson MF. 2001. Consumption choice by bears feeding on salmon. *Oecologia* **127**: 372–82.
- Gende SM, Edwards RT, Willson MF, and Wipfli MS. 2002. Pacific salmon in aquatic and terrestrial ecosystems. *BioScience*. In press.
- Gresh T, Lichatowich J, and Schoonmaker P. 2000. An estimation of historic and current levels of salmon production in the northeast Pacific ecosystem: evidence of a nutrient deficit in the freshwater systems of the Pacific Northwest. *Fisheries* **25**: 15–21.
- Groot C and Margolis L. 1991. Pacific salmon life histories. Vancouver: University of British Columbia Press.
- Gross HP, Wurstbaugh WA, and Luecke C. 1998. The role of anadromous sockeye salmon in the nutrient loading and productivity of Redfish Lake, Idaho. *T Am Fish Soc* **127**: 1–18.
- Hare SR, NJ Mantua, and RC Francis. 1999. Inverse production regimes: Alaska and west coast Pacific salmon. *Fisheries* **24**: 6–14.
- Helfield JM and Naiman RJ. 2001. Effects of salmon-derived nitrogen on riparian forest growth and implications for stream habitat. *Ecology* **82**: 2403–09.
- Hilderbrand GV, Hanley TA, Robbins CT, and Schwartz CC. 1999. Role of brown bears (*Ursus arctos*) in the flow of marine nitrogen into a terrestrial ecosystem. *Oecologia* **121**: 546–50.
- Hilderbrand GV, Schwartz CC, Robbins CT, *et al.* 1999. The importance of meat, particularly salmon, to body size, population productivity, and conservation of North American brown bears. *Can J Zoolog* **77**: 132–38.
- Juday C, Rich WH, Kemmerer GI, and Mann A. 1932. Limnological studies of Karluk Lake, Alaska, 1926–1930. *B Bur Fish Wash* **47**: 407–34.
- Kline TC Jr, Goering JJ, Mathisen OA, and Poe PH. 1990. Recycling of elements transported upstream by runs of Pacific salmon: I. d15N and d13C evidence in Sashin Creek, southeastern Alaska. *Can J Fish Aquat Sci* **47**: 136–44.
- Kline TC Jr, Goering JJ, Mathisen OA, and Poe PH. 1993. Recycling of elements transported upstream by runs of Pacific Salmon: II. d15N and d13C evidence in the Kvichak River Watershed, Bristol Bay, southwestern Alaska. *Can J Fish Aquat Sci* **50**: 2350–65.
- Kondolf GM, Sale MJ, and Wolman MG. 1993. Modification of fluvial gravel size by spawning salmonids. *Water Resour Res* **29**: 2265–74.
- Kroghin EM. 1975. Transport of nutrients by salmon migrating from the sea into lakes. In: AD Hasler (Ed). Coupling of land and water systems. New York: Springer-Verlag.
- Kyle GB. 1996. Stocking sockeye salmon (*Oncorhynchus nerka*) into barren lakes of Alaska: effects on the macrozooplankton. *Fish Res* **28**: 29–44.
- Mantua, NJ, Hare SR, Zhang Y, *et al.* 1997. A Pacific-interdecadal climate oscillation with impacts on salmon production. *Bull Am Meteorol Soc* **78**: 1069–79.
- Minakawa N and Gara RI. 1999. Ecological effects of a chum salmon (*Oncorhynchus keta*) spawning run in a small stream of the Pacific Northwest. *J Freshwater Ecol* **14**: 327–35.
- Montgomery DR, Buffington JM, Peterson NP, *et al.* 1996. Streambed scour, egg burial depths, and the influence of salmonid spawning on bed surface mobility and embryo survival. *Can J Fish Aquat Sci* **53**: 1061–70.
- Naiman RJ, Bilby RE, Schindler DE, and Helfield JM. 2002. Pacific salmon, nutrients, and the dynamics of freshwater and riparian ecosystems. *Ecosystems* **5**: 399–417.
- National Research Council (NRC). 1996. Upstream: salmon and society in the Pacific Northwest. Washington, DC: National Academy Press.
- Obermeyer KE, Hodgson EA, and Willson MF. 1999. American Dipper, *Cinclus mexicanus*, foraging on Pacific salmon, *Oncorhynchus sp.*, eggs. *Can Field Nat* **113**: 288–90.
- Peterson DP and Footo CJ. 2000. Disturbance of small-stream habitat by spawning sockeye salmon in Alaska. *T Am Fish Soc* **129**: 924–34.
- Quinn TP and Kinnison MT. 1999. Size-selective and sex-selective predation by brown bears on sockeye salmon. *Oecologia* **121**: 273–82.
- Quinn TP, Wetzel L, Bishop S, *et al.* 2001. Influence of breeding habitat on bear predation, and age at maturity and sexual dimorphism of sockeye salmon populations. *Can J Zoolog* **79**: 1782–93.
- Reimchen TE. 2000. Some ecological and evolutionary aspects of bear-salmon interactions in coastal British Columbia. *Can J Zoolog* **78**: 448–57.
- Schindler DE, Herwig BR, and Carpenter SR. 2000. Biotic manipulations of aquatic ecosystems. In: Sala OE, Jackson RB, Mooney HA, and Howarth RW (Eds). Methods in ecosystem science. New York: Springer. p 308–17.
- Schindler DE and Lubetkin S. 2003. The use of stable isotopes to quantify nutrient and material transport by organisms. In: Polis GA, Power ME, and Huxel G (Eds). Food webs at the landscape level. Oxford: Oxford University Press. In press.
- Schindler DW. 1998. Replication versus realism: the need for ecosystem-scale experiments. *Ecosystems* **1**: 323–34.
- Schmidt DC, Carlson SR, Kyle GB, and Finney BP. 1998. Influence of carcass-derived nutrients on sockeye salmon productivity of Karluk Lake, Alaska: importance in the assessment of an escapement goal. *N Am J Fish Manage* **18**: 743–63.
- Shuman RF. 1950. Bear depredations on red salmon spawning populations in the Karluk River system, 1947. *J Wildlife Manage* **14**: 1–9.
- Taylor, EB. 1991. A review of local adaptation in Salmonidae, with particular reference to Pacific and Atlantic salmon. *Aquaculture* **98**: 185–207.
- Willson MF, Gende SM, and Marston BH. 1998. Fish and the forest: expanding perspectives on fish-wildlife interactions. *BioScience* **48**: 455–62.
- Wipfli MS, Hudson J, and Caouette J. 1998. Influence of salmon carcasses on stream productivity: response of biofilm and benthic macroinvertebrates in southeastern Alaska, USA. *Can J Fish Aquat Sci* **55**: 1503–11.
- Vander Zanden MJ and Rasmussen JB. 1999. Primary consumer delta C-13 and delta N-15 and the trophic position of aquatic consumers. *Ecology* **80**: 1395–1404.