ECOSYSTEMS

Keystone Interactions: Salmon and Bear in Riparian Forests of Alaska

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ABSTRACT

The term ''keystone species'' is used to describe organisms that exert a disproportionately important influence on the ecosystems in which they live. Analogous concepts such as ''keystone mutualism'' and ''mobile links'' illustrate how, in many cases, the interactions of two or more species produce an effect greater than that of any one species individually. Because of their role in transporting nutrients from the ocean to river and riparian ecosystems, Pacific salmon (*Oncorhynchus* spp.) and brown bear (*Ursus arctos*) have been described as keystone species and mobile links, although few data are available to quantify the importance of this interaction relative to other nutrient vectors. Application of a mass balance model to data from a southwestern Alaskan stream suggests that nitrogen (N) influx to the riparian forest is significantly increased in the presence of both salmon and bear, but not by either species individually. The interactions of salmon and bear may provide up to 24% of riparian N budgets, but this percentage varies in time and space according to variations in salmon escapement, channel morphology and watershed vegetation characteristics, suggesting interdependence and functional redundancy among N sources. These findings illustrate the complexity of interspecific interactions, the importance of linkages across ecosystem boundaries and the necessity of examining the processes and interactions that shape ecological communities, rather than their specific component parts.

Key words: salmon; bear; riparian forest; marine-derived nutrients; nitrogen; keystone species.

INTRODUCTION

''*All animals are equal, but some animals are more equal than others.*''

George Orwell (1945)

Ecological theory holds that certain animals exert a disproportionately important influence on the ecosystems in which they live. Paine (1966) first described this phenomenon in reporting how a predatory starfish (*Pisaster ochraceus*) influences the species composition and population density of an intertidal ecosystem. By eating masses of barnacles, *Pisaster* prevents competitive exclusion by dominant organisms, thereby creating open space for a greater number of species. Paine (1969) subsequently introduced the term ''keystone species'' to describe those animals that control the integrity and stability of their communities. Since then, the concept has been widely used in ecology and conservation, and the keystone designation has been applied to a wide range of taxa at various trophic levels in various ecosystems (see Bond 1993; Mills and others 1993; Power and others 1996).

Although there is no universally accepted operational definition of what constitutes a keystone species, certain requisite traits have been identified. Animals so designated are generally native species that regulate, through their activities and abun-

dances, the productivity, diversity or physical structure of their communities, with influences extending beyond those organisms directly affected through trophic interactions (Paine 1966, 1969). Implicit in the concept is that keystone species are exceptional in their importance relative to the rest of the community (Mills and others 1993), that they are unique in their functioning within the community (Kotliar 2000), and that their impacts are disproportionately large relative to their abundances (Power and others 1996). Loss of a keystone species results in significant changes in the structure or organization of a given ecosystem, presumably with adverse consequences for the survival of other native species or populations.

Most descriptions of the keystone phenomenon focus on a single species, although it is understood that in many cases keystone effects arise through the interactions of two or more species. For example, studies of mutualism (for example, the ''keystone mutualist hypothesis'' *sensu* Gilbert 1980; Christian 2001) and facilitation (for example, Bertness and Shumway 1993; Bertness and Leonard 1997; Mulder and others 2001) demonstrate how positive interactions among different species help maintain the structure and diversity of various plant and animal communities, particularly under adverse environmental conditions. There has been some debate as to whether such positive interactions exert a more widespread influence than do the forces of competition and predation described in Paine's definitive keystone example (Bruno and others 2003), but both paradigms are dependent on interspecific interactions. Use of the term ''interaction strength'' as a measure of the importance of keystone predators (for example, Macarthur 1972; Paine 1992) implies that this importance is derived through the reactions of other species. Accordingly, some authors have argued that ecological complexity and community stability may be more dependent on synergistic effects resulting from interspecific interactions than on the actions or abundances of any one species (Naiman and Rogers 1997; Mills and others 1993; Lawton and Jones 1995; Soulé and others 2003).

In some cases these keystone interactions involve species that migrate across ecosystem boundaries. Examples include the ''mobile link'' pollinators and seed dispersers described by Gilbert (1980), and the spatial subsidies described by Polis and others (1997). Animals that carry nutrients, energy or genetic material among otherwise separate food webs may exert a significant influence on the structure and dynamics of receiving communities, even if they are extrinsic to those communities for most of their life histories (see Lundberg and Moberg 2003).

Another example of this sort of interspecific, trans-boundary interaction is the transfer of nutrients from the Pacific Ocean to river and riparian ecosystems by sockeye salmon (*Oncorhynchus nerka*) and brown bear (*Ursus arctos*). Pacific salmon have been described as keystone species in coastal ecosystems because of their importance as a food resource for vertebrate predators and scavengers (Willson and Halupka 1995; Willson and others 1998). Similarly, salmon and bear have been described as interacting mobile link organisms because of their role in transporting marine-derived nutrients to forest ecosystems in Alaska (Lundberg and Moberg 2003). Although marine-derived nutrients have been shown to influence riparian structure and dynamics (Helfield and Naiman 2001, 2002; Bartz and Naiman 2005), few data are available to quantify the importance of the salmon-bear interaction relative to other nutrient vectors. Here we present a mass balance model for nitrogen (N) flux in the riparian forest adjacent to a boreal Alaskan stream. The objectives of this study are to quantify spatiotemporal variations in N contributions via salmon and bear relative to other N sources, and to elucidate the potential long-term effects of salmon-bear interactions on the productivity and species composition of riparian ecosystems. In so doing, we hope to build on the existing body of theoretical work related to the keystone species concept and enhance our understanding of the ways in which ecological communities are shaped by interspecific interactions and linkages across ecosystem boundaries.

INTERACTIONS OF SALMON, BEAR AND RIPARIAN VEGETATION

Having spent most of their lives feeding and growing at sea, Pacific salmon returning to spawn and die in their natal streams carry marine-derived nutrients in their body tissues. Returning salmon are eaten by numerous mammal and bird species (Cederholm and others 1989; Willson and others 1998), and nutrients from decaying salmon carcasses support the production of periphyton, aquatic macroinvertebrates, resident freshwater fishes and juvenile salmon in spawning streams (Mathisen and others 1988; Kline and others 1990, 1993; Schuldt and Hershey 1995; Michael 1995; Bilby and others 1996, 1998; Wipfli and others 1998). These nutrients are also delivered to terrestrial vegetation. Studies of naturally-occurring stable isotopes indi-

cate that riparian plants adjacent to spawning streams may derive as much as 18–26% of their foliar N from salmon (Bilby and others 1996; Ben-David and others 1998; Hilderbrand and others 1999a; Helfield and Naiman 2001, 2002).

Transfer of marine-derived nutrients from spawning streams to riparian ecosystems is mediated largely by bears. Salmon are an important seasonal food source for coastal bear populations (Hilderbrand and others 1996, 1999b), and bears frequently consume a large proportion of total spawner biomass, either through predation or scavenging of post-spawn carcasses (Quinn and Kinnison 1999; Quinn and Buck 2000; Reimchen 2000; Ruggerone and others 2000; Gende and others 2001; Quinn and others 2001). Marine-derived nutrients are then made available to riparian vegetation through dissemination of partially-eaten salmon carcasses and salmon-enriched wastes. Hilderbrand and others (1999a) report that brown bears on the Kenai Peninsula, Alaska, deliver 83–84% of marine-derived N detected in white spruce (*Picea glauca*) foliage within 500 m of spawning streams. These findings are consistent with other studies demonstrating spatial correlations between bear activity and marine-derived N in riparian foliage (Ben-David and others 1998; Helfield and Naiman 2002).

Although bears are the most visible consumers of salmon, they are not the only species to make use of this anadromous food source. River otter (*Lontra canadensis*) and mink (*Mustela vision*) feed regularly on salmon (Blundell and others 1998; Ben-David and others 1997a), whereas marten (*Martes americana*) incorporate salmon into their diets during years of low abundance of principal prey species (Ben-David and others 1997b). Bald eagle (*Haliaeetus leucocephalus*) and gulls (*Larus* spp.) also scavenge and occasionally kill salmon in Alaskan streams (Ben-David and others 1998; Quinn and Buck 2000). On the Olympic Peninsula of Washington, where brown bear are absent and black bear (*U. americanus*) are relatively scarce, Cederholm and others (1989) list 22 species of mammals and birds known to consume salmon carcasses. These animals all transport marine-derived nutrients and organic matter to terrestrial ecosystems, with amounts and spatial distributions varying according to the abundance, longevity, mobility and per capita salmon consumption of each species.

At finer spatial scales, insects play an important role in mediating stream-riparian nutrient transfer (Jackson and Fisher 1986). Aquatic larvae of numerous stonefly (Plecoptera), caddisfly (Tri-choptera) and midge (Diptera: Chironomidae) species feed directly on salmon carcasses in streams, whereas mayflies (Ephemeroptera), blackflies (Diptera: Simuliidae) and midges feed on fine particles immediately downstream from decomposing carcasses (Minakawa 1997; Wipfli and others 1998; Minakawa and Gara 1999). Salmon-derived nutrients are also incorporated into the body tissues of predatory stoneflies and dragonflies (Odonata) through trophic interactions (Kline and others 1990; Bilby and others 1996). These materials are subsequently transferred to adjacent terrestrial ecosystems with the emergence of the adult insects and their subsequent death or consumption by terrestrial insectivores. Salmon carcasses deposited on exposed gravel bars and in the riparian zone are quickly colonized and consumed by larval forms of terrestrial flies (Diptera: Calliphoridae and Scathophagidae) and carrion beetles (Coleoptera: Silphidae), which may be an important factor controlling decomposition and distribution of salmon-derived nutrients (Meehan 2000).

Marine-derived nutrients are also transferred to riparian habitats through abiotic processes. In larger rivers, flooding deposits salmon carcasses on stream banks (Cederholm and others 1989; Ben-David and others 1998). In streams with hydraulically conductive substrates, dissolved nutrients from decomposing carcasses may be transferred to riparian ecosystems via shallow subsurface (that is, hyporheic) flowpaths. Studies of non-salmon bearing streams have demonstrated that the hyporheic zone can serve as a transient storage area for nutrients, as solutes downwelling from surface water to the hyporheic zone can be rapidly attenuated through physical sorption and uptake by microbial communities (Bencala and Walters 1983; Triska and others 1994). Where hyporheic zones are shallow and extend laterally beyond the active floodplain, the roots of riparian plants may extend into this saturated zone and take up transiently stored nutrients. O'Keefe and Edwards (2003) reported that concentrations of ammonium (NH_4) and soluble reactive phosphorus increased significantly in a southwestern Alaskan stream following entry of spawning sockeye salmon, and that nutrient-enriched surface water subsequently entered the hyporheic zone beneath the riparian forest. The importance of hyporheic exchange as a vector for marine nutrients is controlled by the physical extent and hydraulic conductivity of the hyporheic zone, as well as by the abundance of salmon carcasses within the stream.

This marine nutrient subsidy has a potentially important influence on riparian plant communities.

Recent studies have found that foliar N content, basal area growth and stem densities of riparian trees are enhanced at sites near spawning streams (Helfield and Naiman 2001, 2002; Bartz and Naiman 2005), whereas species richness and density of understory plants are decreased, relative to comparable sites without salmon (Bartz and Naiman 2005). It is possible that marine N influx may also decrease the competitive advantage of N-fixing plants such as alder (*Alnus* spp.), resulting in decreased abundance of these species near spawning streams (Helfield and Naiman 2002). Because plants with higher foliar N contents are generally more nutritious and palatable to browsers such as moose (*Alces alces*) and snowshoe hare (*Lepus americanus*; Bryant 1987; Pastor and others 1988), marine N inputs may also influence patterns of browsing, which in turn affects nutrient cycling, successional processes and plant species composition (Kielland and Bryant 1998; Suominen and others 1999).

The consequences of marine nutrient subsidies to riparian ecosystems also affect aquatic ecosystems. Increased N content in riparian foliage entails increased nutritional quality of litter delivered to the stream, potentially increasing aquatic productivity. Increased growth and density of riparian trees enhances shading, bank stabilization, sediment filtration and production of large woody debris (LWD), all of which enhance spawning and rearing habitat for salmonid fishes (Meehan and others 1977; Harmon and others 1986; Naiman and Décamps 1997; Bilby and Bisson 1998; Naiman and others 1998). Because LWD is a key structural element retaining salmon carcasses in streams (Cederholm and Peterson 1985), increased riparian production further enhances the availability of salmon carcasses and associated nutritive effects in lotic ecosystems. As a result of these linkages, nutrients carried upstream by adult salmon help to enhance the productivity of subsequent generations of salmon and other stream-dwelling fishes.

A MASS BALANCE MODEL FOR RIPARIAN N AT LYNX CREEK

The mass balance model estimates N flux at Lynx Creek, a tributary of the Wood River Lakes system in the Bristol Bay region of southwestern Alaska, USA (59°29′ N, 158°55′ W). The area is in a transitional climatic zone, with maritime as well as continental influences affecting weather patterns. Average summer temperatures range from 6 to 20°C, and average winter temperatures range from

−15 to −6°C. Annual precipitation ranges from 250 to 340 cm, of which 200–250 cm falls as snow (Hartman and Johnson 1984). Lynx Creek is approximately 2.3 km long, originating at Lynx Lake and discharging into Lake Nerka. Mean summer discharge is approximately 500 l s^{-1} (O'Keefe and Edwards 2003). Including Lynx Lake and its tributaries, the Lynx Creek watershed covers approximately 2760 ha (USGS 1979). The riparian vegetation is a boreal forest association of white spruce and paper birch (*Betula papyrifera*) interspersed with stands of balsam poplar (*Populus balsamifera*), willow (*Salix* spp.) and cottongrass (*Eriophorum* spp.). Upland hillslopes are dominated by dense stands of green alder (*Alnus crispa*).

Since 1947, annual escapement of sockeye salmon to Lynx Creek has ranged from 464 to 17,023 (mean = 3,084), with spawning occurring from late July through August (Rogers and Rogers 1998). Given that the average adult sockeye contains approximately 82 g of N in its body tissues (Larkin and Slaney 1997), annual spawning runs bring approximately 38–1,397 kg N (mean = 253) to the Lynx Creek watershed during the growing season. The area supports a population of approximately 2.8 bears per 100 km^2 (Van Daele 1998), all of whom feed on salmon throughout the spawning season. Recent studies have characterized patterns of bear predation on sockeye (Quinn and Buck 2000; Ruggerone and others 2000; Gende and others 2001; Quinn and others 2001), as well as hyporheic processes (O'Keefe and Edwards 2003) and marine-derived N enrichment of riparian vegetation (Helfield and Naiman 2002; Bartz and Naiman 2005) in the Wood River system.

The mass balance model calculates N influx to a 200 m-wide corridor (45.2 ha) of riparian forest on either side of Lynx Creek. Specifically, the model estimates annual contributions of marine-derived N via bear activity and hyporheic exchange for comparison with contributions from non-marine sources (that is, precipitation, leaching from upland soils and N fixation). For each N source, the model defines environmental parameters and identifies variables controlling N fluxes. Parameters may then be adjusted to estimate N fluxes under different scenarios.

Input data were derived from empirical observations. Where data from Lynx Creek were not available, we used data from comparable sites within the Wood River system or ranges of published values for boreal Alaskan ecosystems. Minimum, maximum and mean values were identified for all input variables. Model calculations were then performed repeatedly, using all possible combinations of input data so as to generate the full range of

possible results for each N source. Mean values for results were obtained using mean values for all input variables. To assess the importance of salmon-bear interactions, we calculated total annual N influx under 1,296 scenarios representing all possible combinations of minimum, maximum and mean contributions from each N source, assuming the presence of both salmon and bear (729 scenarios), bear but not salmon (243 scenarios), salmon but not bear (243 scenarios), and neither salmon nor bear (81 scenarios). Differences among scenarios were evaluated with Kruskal-Wallis analyses of variance using ranks, followed by Dunn's multiple contrast hypothesis test. Calculations, assumptions and input data are described below. Sample calculations using mean input data are provided in Appendix A (http://www.springerlink.com).

Precipitation

Precipitation is a variable but continuous source of N in boreal forests. No data are available describing atmospheric deposition of N within the Wood River system, but the US National Atmospheric Deposition Program (NADP 2003) reports a mean annual flux of 0.19 kg ha^{-1} (range = 0.02 –0.63) for the years 1980 – 2001 at each of its two closest monitoring sites (AK01 Poker Creek; AK03 Denali National Park). Although these sites are in the interior of Alaska and receive less annual rainfall than does the Bristol Bay region (NADP 2003; Hartman and Johnson 1984), studies of global patterns of N cycling indicate that they receive comparable, or slightly greater, amounts of reactive N via atmospheric deposition (Galloway and Cowling 2002). Using these data, the model calculates N influx via precipitation as

$$N_P = J_P \cdot A_R \qquad (1)$$

where N_P is the mass of N delivered annually via precipitation, J_P is the per unit area annual flux of N via precipitation, and A_R is the area of the riparian zone.

Leaching from Upland Soils

Riparian forests are areas of net nutrient accumulation within the watershed (Van Cleve and Yarie 1986) and typically derive significant proportions of their total nutrient budgets from upland soils. Whereas surface runoff is likely negligible in the undisturbed, forested Lynx Creek watershed, leaching and downslope movement of soil solution may be important vectors for N. Excluding the lake and its tributaries, the Lynx Creek watershed comprises approximately 273 ha of upland area

with potential to export N to the riparian zone via downslope leaching (USGS 1979). In a study of nutrient cycling at forest sites encompassing much of the range of conditions encountered in boreal Alaska, Van Cleve and others (1983) report mean annual fluxes ranging from 0.4 to 1.9 kg N ha^{-1} (all-site mean = 1.2) via leaching. This range encompasses values reported in subsequent studies (Kaye and others 2003). Using these data, leaching contributions at Lynx Creek are calculated as

$$N_L = J_L \cdot A_L \qquad (2)$$

where N_L is the mass of N delivered annually via leaching from upland soils, J_L is the per unit area annual flux of N via leaching, and A_L is the upland leaching area.

N Fixation

Biological N fixation may be an important source of N in northern forests. Through symbiosis with the *Frankia* actinomycete, alders fix atmospheric N_2, which is converted to ammonium and transferred to surrounding soils via root and nodule secretions and production of N-rich leaf litter (Binkley 1986; Wurtz 2000). This process results in accelerated N cycling and increased N availability in forest soils, as well as in increased growth and foliar N content in sympatric conifers and understory plants (Binkley 1983; Binkley and others 1985, 1992; Wurtz 1995; Vogel and Gower 1998; Rhoades and others 2001). Shrub alders of boreal ecosystems (for example, *A. crispa; A. tenuifolia*) inhabit early-successional forests (Van Cleve and others 1971; Van Cleve and Viereck 1981; Wurtz 1995), but also form long-term, stable communities (Wilson and others 1985; Wurtz 2000), which may influence soil N dynamics throughout the later stages of succession.

No data are available describing N fixation at Lynx Creek, but other studies have characterized rates of N fixation in boreal Alaskan forests. Van Cleve and others (1971) report a mean annual N fixation rate of 156 kg ha^{-1} (range = 72 – 362) for alder stands of various ages within the Tanana River floodplain. These values are similar to those reported in subsequent studies in the area (Klingensmith and Van Cleve 1993) and at other boreal and Alaskan sites (Lawrence 1958; Daly 1966). Assuming that N fixation rates are comparable at Lynx Creek and proportionate with alder abundance, N fixation may be calculated as

$$J_a = a \cdot (J_{aref} / a_{ref}) \qquad (3)$$

where J_a is the per unit area annual flux of N via N fixation, a is alder abundance (that is, proportion of

cover or aboveground forest biomass), J_{aref} is the per unit area annual flux of N via N fixation at the reference site (for example, Van Cleve and others 1971), and a_{ref} is alder abundance at the reference site. Alder comprises 83 – 89% (mean = 86) of total aboveground plant biomass at the Tanana River sites (Van Cleve and others 1971). As alder abundance data for Lynx Creek are reported in terms of percent cover, this calculation uses percent cover as a surrogate for percent biomass (see Mynemi and others 2001; Fensham and others 2002).

Alder covers approximately 44% of the Lynx Creek watershed (O'Keefe and Edwards 2003), but alder abundance in the riparian zone is negligible (Helfield and Naiman 2002). The majority of alder-fixed N affecting the Lynx Creek riparian forest is therefore leached from upland stands. Mean annual leaching losses described by Van Cleve and others (1983) represent approximately 0.2% of forest floor soil N pools. Assuming a similar rate of leaching at Lynx Creek, total riparian N influx via N fixation is calculated as

$$N_a = (J_{\text{aU}} \cdot p_{\text{L}} \cdot A_{\text{L}}) + (J_{\text{aR}} \cdot A_{\text{R}}) \qquad (4)$$

where N_a is the mass of N delivered annually via N fixation, J_{aU} is the per unit area annual flux of N via upland fixation, calculated as in Eq. (3), p_{L} is the proportion of soil N lost to leaching, A_{L} is the upland leaching area, J_{aR} is the per unit area annual flux of N via riparian N fixation, calculated as in Eq. (3), and A_{R} is the area of the riparian zone. This calculation assumes upland alder distribution to be relatively homogenous (that is, non-patchy).

Although alder is the primary N-fixing species in Alaska's boreal forests (Wurtz 1995), there are other organisms capable of fixing N. For example, the ubiquitous Schreber's feather moss (*Pleurozium schreberi*) forms symbioses with cyanobacteria (*Nostoc* spp.) and may fix as much as 1.5 – 2 kg N ha^{-1} annually in mid- to late-successional boreal forests, depending on abundance and the length of the growing season (DeLuca and others 2002). Similarly, some lichen mycobionts form symbioses with cyanobacteria and fix N (Rai 1988; Honegger 1991). However, rates of N fixation by lichens and bryophytes are 1 – 2 orders of magnitude lower than those reported for alder (for example, Alexander and Billington 1986; Van Cleve and others 1971), and N fixed by lichens and bryophytes may be less likely to be exported to soil N pools. Previous studies suggest that bryophytes fix barely enough N to satisfy their own metabolic requirements (Alexander and Billington 1981), and that N transfer from feather moss to neighbouring trees or

shrubs is tortuous (Van Cleve and Alexander 1981). Similarly, a relatively large proportion of N fixed by lichens is retained for cyanobacterial metabolism (Rai and others 1983). Nonetheless, it should be recognized that the mass balance model underestimates total biological N fixation by considering only alder-mediated N fixation.

Hyporheic Exchange

O'Keefe and Edwards (2003) confirmed the existence of an extensive parafluvial hyporheic zone adjacent to Lynx Creek and demonstrated that hyporheic exchange is a feasible mechanism for transporting marine-derived nutrients to riparian vegetation. Following a spawning run of 9460 sockeye in 2000 (T. P. Quinn, unpublished data), a flux of 4.3 kg N ha^{-1} yr^{-1} was observed moving through a 100-cm deep column of hyporheic water adjacent to Lynx Creek (R. T. Edwards and T. C. O'Keefe, unpublished data). Assuming a proportional relationship between sockeye escapement and the mass of N downwelling into hyporheic flowpaths, annual flux may be calculated as

$$J_{\text{H}} = E \cdot (J_{\text{Href}} / E_{\text{ref}}) \qquad (5)$$

where J_{H} is the per unit area annual flux of N per 100 cm deep column of hyporheic water, E is escapement, J_{Href} is the per unit area flux of N per 100 cm deep column of hyporheic water observed during the reference year (for example, 2000), and E_{ref} is escapement during the reference year.

The depth to the parafluvial hyporheic zone adjacent to Lynx Creek ranges from 30 to 150 cm below the soil surface (O'Keefe and Edwards 2003). Because the maximum rooting depth of white spruce is approximately 120 cm (Nienstaedt and Zasada 1990), only the upper portion of the hyporheic water column is accessible for uptake, and in some cases none of it is accessible. Accessible hyporheic flux is therefore calculated as

$$J_{\text{Hacc}} = J_{\text{H}} \cdot [(Z_{\text{rt}} - Z_{\text{H}}) / 100] \qquad (6)$$

where J_{Hacc} is the per unit area flux of hyporheic N accessible to riparian plants, J_{H} is the flux of hyporheic N as in Eq. (5), Z_{rt} is the rooting depth of riparian plants, and Z_{H} is the depth to the hyporheic zone. On average, the parafluvial hyporheic zone extends 35 m (range = 0 – 100) beyond the active channel at Lynx Creek (R. T. Edwards and T. C. O'Keefe, unpublished data). As the spatial extent and configuration of the hyporheic zone varies according to reach-scale variations in channel morphology and substrate permeability (Edwards 1998), the riparian

area underlaid by hyporheic flows at Lynx Creek may range from 0 to 45.2 ha. Hyporheic N contributions are therefore calculated as

$$N_H = J_{Hacc} \cdot A_H \qquad (7)$$

where N_H is the mass of N delivered annually to riparian plants via hyporheic exchange, J_{Hacc} is the flux of accessible hyporheic N as in Eq. (6), and A_H is the area of the parafluvial hyporheic zone, calculated as the product of stream length and twice the lateral extent of hyporheic flow beyond the active channel.

Bear Activity

Bear density in the northern Bristol Bay region is approximately 2.8 individuals per 100 km² (Van Daele 1998), with densities ranging from 0.53 to 30.4 individuals per 100 km² throughout interior Alaska (Van Daele and others 2001). Local densities near streams are typically greater during salmon spawning. For example, Hilderbrand and others (1999a) reported 43–57% of bear observations on the Kenai Peninsula as being within 500 m of spawning streams. Assuming a similar degree of aggregation at Lynx Creek, bear density may be calculated as

$$B_{agg} = B \cdot (p_{BF} / p_{AF}) \qquad (8)$$

where B_{agg} is local bear density during spawning season, B is regional bear density, p_{BF} is the proportion of bears observed within 500 m of spawning streams, and p_{AF} is the proportion of the total area observed that is within 500 m of spawning streams (Hilderbrand and others 1999a). In the absence of salmon, the model assumes no bear aggregation (that is, $B_{agg} = B$).

On average, bears kill approximately 37% of sockeye spawning in the Wood River system (Quinn and others 2001), but predation rates vary from year to year according to bear density and salmon abundance (Quinn and Kinnison 1999; Ruggerone and others 2000; Quinn and others 2001). At Hansen Creek, another tributary of the Wood River system that is comparable in length and average escapement to Lynx Creek (Rogers and Rogers 1998), Ruggerone and others (2000) report an inverse relationship between escapement and the proportion of salmon killed by bears. This relationship is quantified as

$$p_{BK} = (2493 \cdot E^{-0.531}) / 100 \qquad (9)$$

where p_{BK} is the proportion of salmon killed by bears and E is escapement (Ruggerone and others 2000). The proportion of biomass eaten per fish

also varies according to salmon abundance and ease of capture, with a greater proportion eaten when fish are less abundant or harder to capture (Gende and others 2001). Gende and others (2001) report that percent consumption per fish killed ranges from 4 to 80 (all-site mean = 25) within the Wood River system. Assuming the uneaten portion of each bear-killed salmon is left on the riparian forest floor, N influx via discarded salmon carcasses may be calculated as

$$N_{carc} = E \cdot p_{BK} \cdot (1 - p_{eat}) \cdot m_{Nsock} \qquad (10)$$

where N_{carc} is the mass of N delivered annually via deposition of partially-eaten salmon carcasses, E is escapement, p_{BK} is the proportion of salmon killed by bears as in Eq. (9), p_{eat} is the proportion of biomass eaten per fish, and m_{Nsock} is the mass of N contained in the body tissues of each adult sockeye salmon (Larkin and Slaney 1997).

The other means by which bear contribute N to riparian forests is via waste excretion. Among Kenai Peninsula bears observed within 500 m of spawning streams, Hilderbrand and others (1999a) report that each adult female passes 0.046–0.051 kg ha^{-1} of salmon-derived N annually via urine and, to a lesser extent, feces and decomposition of body tissues after death. On average, salmon represent 62% of dietary carbon and N for Kenai Peninsula bears, with values for coastal, salmon-eating populations in Alaska ranging from 33 to 79% (Hilderbrand and others 1999b). Using these data, N influx via bear excretion may be calculated as

$$J_{excr} = J_{Mexcr} / p_{Ndiet} \qquad (11)$$

where J_{excr} is the per unit area excretion of N per bear, J_{Mexcr} is the per unit area excretion of salmon-derived N per bear, and p_{Ndiet} is the proportion of bear dietary N derived from salmon. In the absence of salmon, the model calculates this flux as the difference between J_{excr} and J_{Mexcr}. Annual N contributions via bear excretion are then calculated as

$$N_{excr} = (B_{agg} \cdot A_F) \cdot J_{excr} \cdot A_R \qquad (12)$$

where N_{excr} is the mass of N delivered annually via bear excretion, B_{agg} is local bear density as in Eq. (8), A_F is the area within 500 m of the stream, J_{excr} is the per unit area excretion of N per bear as in Eq. (11), and A_R is the riparian area over which this flux is deposited. Total bear-mediated N contributions are calculated as

$$N_B = N_{carc} + N_{excr} \qquad (13)$$

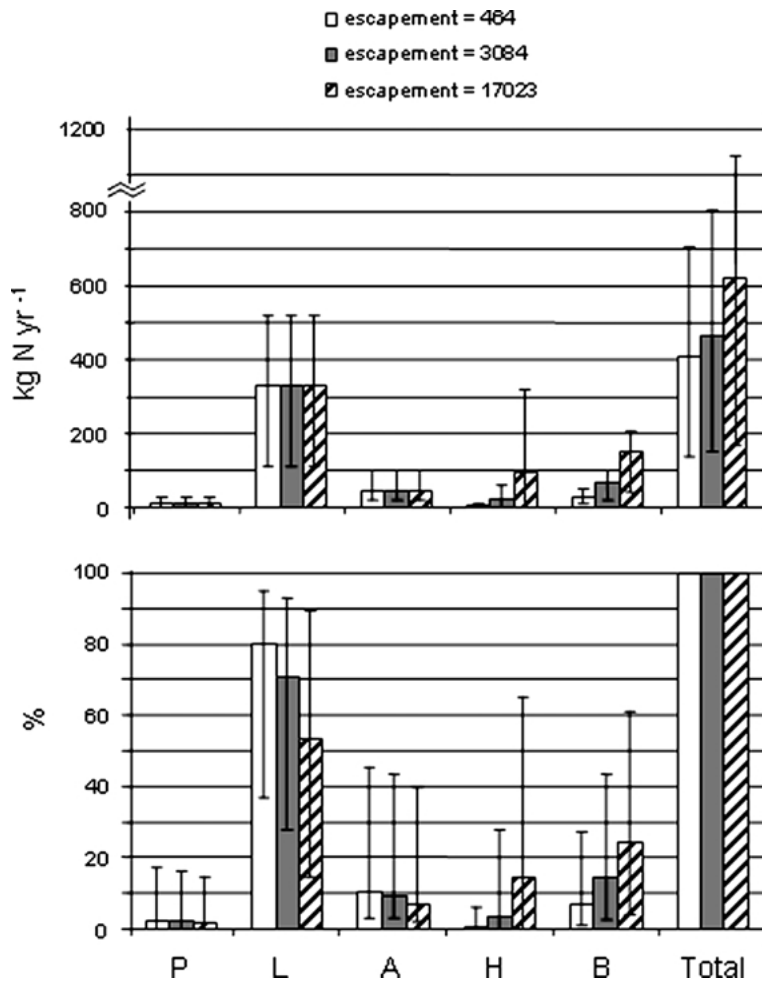where N_B is the mass of N delivered annually via bear activity, N_{carc} is the mass of N delivered via

Figure 1. Estimated annual nitrogen contributions (kg N yr^{-1}) and percentage of total annual nitrogen influx (%) to the riparian zone of Lynx Creek via precipitation (*P*), leaching from upland soils (*L*), alder-mediated nitrogen fixation (*A*), hyporheic exchange (*H*), and bear activity (*B*), as a function of salmon escapement. Data are mean values, calculated by the mass balance model using mean values for all input variables within the parameters of each escapement scenario. Error bars represent the full range of results obtained using all possible combinations of input values.

discarded salmon carcasses as in Eq. (10), and N_{excr} is the mass of N delivered via excretion as in Eq. (12).

Model Results and Discussion

Model calculations indicate that leaching is the dominant source of N in the riparian zone at Lynx Creek (Figure 1). Annual contributions from leaching and other non-marine sources (that is, precipitation and N-fixation) are not influenced by changes in salmon abundance, but these decrease in importance as contributions from marine sources (that is, hyporheic exchange and bear activity) increase with increasing levels of escapement. At minimum levels of escapement, marine-derived N accounts for approximately 7% of total annual riparian N influx. At maximum levels of escapement, this percentage increases to 39%.

When salmon are abundant, bear activity represents the second most important source of riparian N, accounting for an average of 15% of total N influx at mean levels of escapement and 24% at maximum levels of escapement (Figure 1).

Model calculations indicate that during the spawning season there are, on average, 8.4 bears per 100 km^2 within the vicinity of Lynx Creek, and that bears kill approximately 35% of returning spawners in years of mean escapement. This corroborates the mean value (37%) reported for Wood River streams by Quinn and others (2001). The majority of bear-mediated N is distributed via partially-eaten salmon carcasses (that is, ort). In years of mean escapement, bears discard an average of 66 kg N yr^{-1} in ort, as compared with 0.7 kg N yr^{-1} passed in urine and feces. Although a greater mass of N is distributed via ort, N distributed via excretion is more widespread. Carcass scraps are found almost exclusively within the immediate vicinity of spawning streams (Helfield and Naiman 2002), whereas bear excretion may be detected more than 500 m from the stream (Hilderbrand and others 1999a). Moreover, because the majority of excreted N is delivered in urine, which rapidly converts to ammonium (Hilderbrand and others 1999a), excreted N may be more readily available to riparian

trees than organic forms of N bound in carcass tissues (Schulze and others 1994).

It should be recognized that bear activity is not homogenously distributed in the riparian zone. Certain locations adjacent to spawning streams are preferred for fishing and feeding on salmon, and these are characterized by significantly elevated rates of excretion and carcass deposition (Hilderbrand and others 1999a; Helfield and Naiman 2002). By not accounting for localized effects in these bear middens, the mass balance model may underestimate the importance of bear-mediated N at smaller (for example, patch-level) spatial scales.

The importance of bear activity as a source of N is derived through interactions with salmon. Conversely, the importance of salmon-derived N to riparian forests is dependent on facilitation by bear. Model simulations indicate that total N influx to the riparian zone at Lynx Creek is significantly increased in the presence of both salmon and bear, but not in the presence of either salmon or bear alone (Figure 2). These findings suggest that the interactions of salmon and bear are more important to riparian N budgets, and by extension to riparian ecosystems, than are the actions of either species individually.

Although salmon-bear interactions are generally the greatest source of marine-derived N in the riparian zone at Lynx Creek, there are circumstances under which hyporheic contributions may be equally if not more important. The magnitude of N flux via hyporheic exchange is controlled largely by the depth to and lateral extent of hyporheic flowpaths, which are in turn controlled by topography, channel geomorphology, soil texture and hydraulic conductivity (Edwards 1998), all of which vary spatially within the watershed. At the maximum depths and minimum lateral extents observed at Lynx Creek, hyporheic flows are below the reach of riparian roots or confined to the area directly beneath the active channel, so that N influx via hyporheic exchange is nonexistent. In contrast, annual N contributions may be as high as 316 kg, or 65% of total influx in areas where hyporheic flowpaths are at minimum depth and maximum lateral extent (Figure 1). Hyporheic exchange might therefore be a dominant source of N in other systems or within some reaches of Lynx Creek.

Temporal variability in hyporheic exchange might also be greater than indicated by the mass balance model. The mass of dissolved nutrients downwelling to hyporheic flowpaths increases with escapement, but this relationship might not be proportionate. When escapement is high, a large
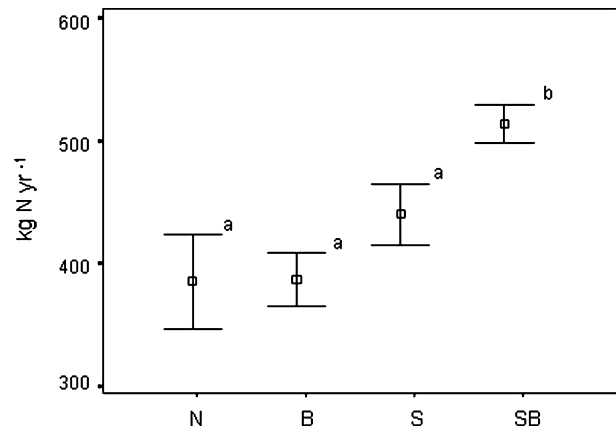

Figure 2. Estimated total annual nitrogen influx (kg N yr^{-1}) to the riparian zone of Lynx Creek, assuming the presence of neither salmon nor bear (*N*), bear but not salmon (*B*), salmon but not bear (*S*), and both salmon and bear (*SB*). Data are mean values ± 95% confidence intervals, based on mass balance calculations for 1,296 scenarios representing all possible combinations of minimum, maximum and mean N contributions from each N source. Superscript letters denote homogenous subsets. Kruskal-Wallis analysis of variance by ranks indicates significant differences among means ($\chi^2_3 = 89.86$, $P < 0.001$). Dunn's multiple contrast tests indicate significant differences between *SB* and *N* ($Q_4 = 5.42$, $P < 0.001$), but not between *B* and *N* ($Q_4 = 0.20$, $P > 0.5$) or *S* and *N* ($Q_4 = 2.26$, $0.2 > P > 0.1$).

proportion of spawner biomass will decompose instream and potentially downwell into the hyporheic zone. When escapement is low, however, bears and other terrestrial piscivores consume a greater proportion of spawner biomass (Ruggerone and others 2000; Gende and others 2001), leaving a disproportionately small amount of carcass material to decompose instream. Accordingly, the importance of hyporheic exchange may be overestimated for years of low escapement and underestimated for years of high escapement.

Although alder-mediated N fixation contributes a relatively small proportion of total riparian N influx at Lynx Creek (Figure 1), this process may be the dominant source of N at other sites. Among other sub-basins within the Wood River system, alder coverage ranges from 5 to 82% in the uplands (T. C. O'Keefe and R. T. Edwards, unpublished data) and from 0 to 19% in riparian zones (Helfield and Naiman 2002). When these parameters are applied to the Lynx Creek model, results indicate that annual N contributions from alder could theoretically be as high as 3,800 kg, accounting for 97% of total influx, or as little as 2 kg, accounting for less than 1% of total influx (Figure 3). Riparian
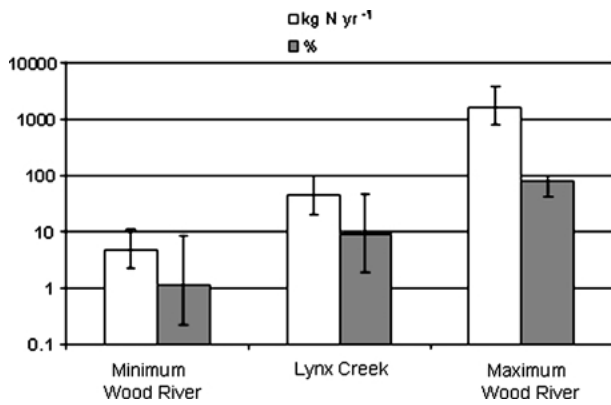
Figure 3. Estimated annual nitrogen contributions (kg N y^{-1}) and percentage of total annual nitrogen influx (%) to riparian zones via alder-mediated nitrogen fixation. Data are presented for Lynx Creek (alder = 50% of watershed area, 0% of riparian area) and for theoretical sites representing the minimum (5% watershed, 0% riparian) and maximum (82% watershed, 19% riparian) alder abundances observed within the Wood River system (Helfield and Naiman 2002; R. T. Edwards and T. C. O'Keefe, unpublished data). Data are mean values, calculated by the mass balance model using mean values for all input variables within the parameters of each scenario. *Error bars* represent the full range of results obtained using all possible combinations of input values.

alder abundance is the most important factor affecting alder-related N contributions, with each 1% increase in riparian alder abundance resulting in an increase of approximately 80 kg in annual N contributions.

KEYSTONE INTERACTIONS: PROCESSES VERSUS PARTS

Salmon and bear meet the basic criteria of keystone species in that their loss entails significant changes in the N budget and, by extension, the productivity and structure of the riparian forest. Organisms affected include terrestrial plants, scavengers, decomposers and browsers, as well as stream-dwelling fishes (Figure 4). To the extent that bear rely on salmon as an essential food source, and to the extent that bear-mediated fertilization of riparian forests helps to enhance habitat for juvenile salmonids, salmon and bear populations are mutually dependent not only in their role as nutrient vectors, but also for their long-term persistence. These findings illustrate the complexity of interspecific linkages and interactions structuring river and riparian ecosystems.

Yet the significance of this keystone interaction varies both temporally and spatially. The impor-

tance of marine-derived N and the relative importance of different N vectors vary from year to year according to variations in escapement and other ecological and climatic parameters (for example, bear abundance, precipitation). Seasonal patterns might also be important. For example, precipitation and leaching occur throughout the year, and a large proportion of N deposited in winter may be lost to the system during the spring thaw. In contrast, marine-derived N is deposited primarily during the growing season, and a greater proportion of annual influx may therefore be retained and assimilated by riparian plants. Spatially, bear excretion and dissemination of salmon carcasses occur at varying degrees of aggregation, whereas rates of hyporheic exchange and leaching vary according to reach-scale differences in topography, soil texture and microbial N processing. In general, the influence of marine-derived N increases with proximity to the stream channel (Ben David and others 1998; Hilderbrand and others 1999a; Helfield and Naiman 2001, 2002), but at broader resolutions, differences in climatic and biogeographic factors (for example, alder abundance, bear density) entail significant differences in the relative importance of N sources.

Moreover, despite their interdependence, the species involved in this interaction are to some extent interchangeable. Marine nutrients may be carried upstream by various species of salmon, including those with typically low spawning densities (for example, Schuldt and Hershey 1995; Bilby and others 1996), or by other anadromous fishes, such as char (*Salvelinus* spp.) or smelt (*Thaleichthys* spp.; Willson and others 1998). Similarly, bears may be the dominant vectors for stream-riparian transfer of marine nutrients in many Alaskan watersheds, but this function may be supplemented (Ben-David and others 1997a, b; Quinn and Buck 2000; Blundell and others 2003) or, in regions where bears are scarce, replaced by other species (Cederholm and others 1989; Bilby and others 1996). Long-term nutrient cycling in salmon-bearing watersheds might therefore depend on a combination of different species and abiotic processes (for example, hyporheic exchange), which alternate over time in their relative functional importance. Although none of these is entirely unique in its function, loss of any one will have long-term if not immediate consequences.

Another reason why this interaction is not easily characterized in terms of the keystone species concept is its reliance on linkages across ecosystem boundaries. Assessing the impact of a given species or guild relative to its abundance within the community implies an ability to discern the boundaries
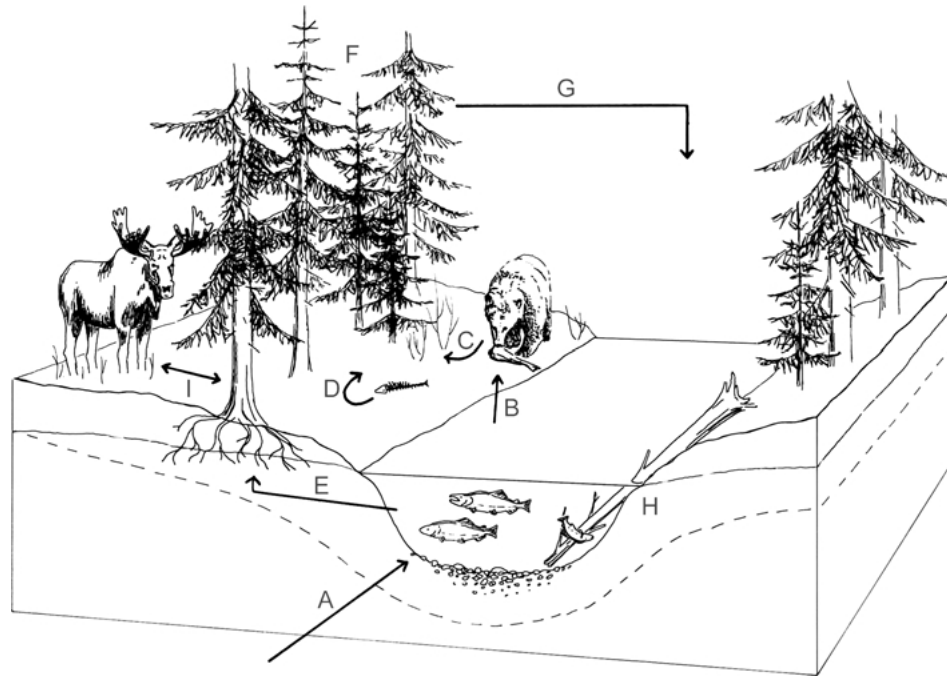
Figure 4. Cycling of marine-derived nitrogen (MDN) and effects on river and riparian ecosystems; (*A*) Spawning salmon transport MDN upstream; (*B*) Bears and other piscivores consume salmon; (*C*) Bears and other piscivores disseminate salmon-enriched wastes and partially-eaten salmon carcasses in the riparian forest; (*D*) Terrestrial and aquatic insects colonize salmon carcasses, enhancing decomposition and MDN diffusion; (*E*) Dissolved N downwells into hyporheic flowpaths beneath the riparian forest and is taken up by tree roots; (*F*) MDN inputs enhance foliar N content and growth rates of riparian trees; (*G*) Riparian trees provide shade, bank stabilization, allochthonous organic matter and large woody debris (LWD), enhancing the quality of instream habitat for salmonid fishes; (*H*) LWD retains post-spawn salmon carcasses in streams, further enhancing MDN availability; (*I*) Increased foliar N content enhances palatability and nutrition of riparian plants, potentially altering patterns of browsing, which in turn affects patterns of riparian productivity and species composition.

of that community (for example, Paine 1992; Power and others 1996; Hurlbert 1997). This is easier to accomplish for sessile organisms in an intertidal community (for example, Paine 1966) than for animals like salmon and bear that migrate over long distances spanning marine, freshwater and terrestrial habitats. As with functional importance, the definition of a community is sensitive to the spatial and temporal scales of observation. Riverine ecosystems are especially characterized by connectivity with surrounding landscapes (Naiman and others 1987; Ward 1989), although even seemingly discrete ecosystems are invariably affected to some degree by external influences.

Despite, or possibly because of, its importance as a theoretical construct, the keystone species concept has been the subject of considerable debate. Whereas some authors have recommended that keystone species be made the focus of environmental management and conservation efforts (for example, Conway 1989; Woodruff 1989; Rohlf 1991; Carroll 1992), others have questioned the applicability of the keystone species concept be-

cause of the difficulties inherent in quantifying keystone effects and distinguishing which species merit such distinction (Mills and others 1993; Hurlbert 1997; Kotliar 2000). Our findings illustrate the extent to which keystone species rely on interspecific interactions and linkages across ecosystem boundaries, and the extent to which their functional importance varies in time and space. Losses of species identified as keystones may have adverse consequences for other members of their communities, but protection of these species does not guarantee the avoidance of such consequences. Accordingly, it may be more constructive to consider the interactions and processes that structure those communities rather than their specific component parts. The search for and protection of keystone species implies a tacit permission to ignore other, more obscure but potentially important taxa, along with interspecific interactions and abiotic processes linking multiple ecosystems, any combination of which may be essential for maintaining the long-term productivity, diversity, physical structure or viability of a given commu-

nity. If the first rule of intelligent tinkering is to save all the parts (Leopold 1953), the second rule should be to understand how they fit together.

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