Importance of salmon to wildlife: Implications for integrated management

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Abstract: Salmon (*Oncorhynchus* spp.) are an important resource for terrestrial wildlife. However, the salmon requirements of wildlife populations and the role wildlife play in nutrient transport across ecosystems are largely ignored in salmon and habitat management. Any activity that reduces the availability of or access to salmon by wildlife may adversely affect wildlife populations and, potentially, ecosystem-level processes. Thus, when the conservation of specific wildlife populations or healthy ecosystems is the management objective, allocation of salmon to wildlife should be considered. We provide an example of how such allocations could be calculated for a hypothetical bear population. Ultimately, salmon allocation for wildlife calls for integrated management of natural resources across agencies, across species, and across ecosystems. We summarize the current state of knowledge relative to the interaction between Pacific salmon and the terrestrial ecosystem, with special emphasis on the import of salmon to terrestrial wildlife and the import of wildlife to terrestrial and aquatic ecosystems.

Key words: allocation, bear, consumer, ecosystem, management, nutrient flow, *Oncorhynchus*, predation, salmon, *Ursus*

Ecology of salmon–wildlife interactions

Nutrient flow across ecosystems: the role of spawning salmon

Nutrients flow within and between ecosystems as part of natural meteorological, geological, and biological processes (Likens and Bormann 1974). Recently, increased attention has been paid to the flow of marine nutrients into freshwater and terrestrial ecosystems through the vehicle of anadromous salmon. In actuality, this complex relationship between the two ecosystems impacts the productivity of the marine system as well as the freshwater and terrestrial systems (Willson et al. 1998, Cederholm et al. 2000). Due to the importance of salmon and the nutrients they transport, they have been suggested as a keystone species in many coastal terrestrial ecosystems of the Pacific rim (Willson and Halupka 1995).

As salmon grow in the marine environment, they accumulate more than 99% of the carbon (C), nitrogen (N), and phosphorous (P) in their body tissues (Mathisen et al. 1988). When salmon return to spawn, they transport these nutrients to the freshwater and terrestrial ecosystems through deposition of eggs and decomposition of carcasses, and through consumers that eat live and dead salmon and subsequently deposit these materials through urine, feces, and decomposition. Although some of these nutrients are swept back out to sea with the flow of fresh water, the return of anadromous salmon ultimately results in a net influx of marine-derived nutrients to the freshwater and terrestrial ecosystems. This influx of marine nutrients can be ecologically significant, because many northern freshwater and terrestrial ecosystems are nutrient limited, and nutrient inputs increase productivity (Chapin et al. 1986, Kyle 1994, Perrin and Richardson 1997).

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Importance of marine nutrients to freshwater ecosystems

Several studies have assessed the flow of marine nutrients into freshwater ecosystems and their effect on productivity. In particular, the recent use of stable isotope tracers has greatly enhanced the ability of researchers to trace the flow of marine-derived nutrients into rivers, lakes, and streams. Mathisen et al. (1988) traced the flow of marine nutrients through the food chain of the Kvichak River watershed and Illiamna Lake, Alaska, finding strong evidence that salmon play a major role in nitrogen dynamics. The return of spawning salmon has also been important in supporting the nutrient requirements, particularly nitrogen, of periphyton, juvenile salmon, and resident fishes (Kline et al. 1990, Kline et al. 1993). Growth rates of juvenile fish in streams containing spawning coho salmon (*Oncorhynchus kisutch*) were double those that lacked returning fish, and the proportion of salmon-contributed nitrogen in the tissues of freshwater biota ranged from 17 to 30% across trophic levels (Bilby et al. 1996).

Importance of marine nutrients to terrestrial vegetation

In addition to their importance to freshwater ecosystems, the nutrients delivered by salmon play a significant ecological role in the terrestrial ecosystem by affecting the productivity of riparian vegetation surrounding streams. Bilby et al. (1996) reported that 17.5% of the nitrogen in riparian foliage along an anadromous stream in Washington was marine in origin. Similarly, Hilderbrand et al. (1999a) found that 15.5 and 17.8% of the nitrogen in trees within 500 m of 2 separate anadromous streams on the Kenai Peninsula, Alaska, was marine-derived. Helfield and Naiman (2001) assessed the isotopic signatures of riparian shrubs and trees near 2 watersheds on Chichigof Island, Alaska. Sitka spruce (*Picea sitchensis*), devil's club (*Oplopanax horridus*), and fern (*Dryopteris dilatata* and *Athyrium filix-femina*) found near spawning sites received 22–24% of their nitrogen from spawning salmon. Only red-alder (*Alnus rubra*), a nitrogen-fixing plant, did not receive a significant proportion of its nitrogen from salmon. In addition to the marine-derived nitrogen content of the Sitka spruce, Helfield and Naiman (2001) reported that growth rates of the spruce were more than 3 times greater at spawning sites than non-spawning sites.

Salmon consumption by wildlife

Returning adult salmon, salmon carcasses, and juvenile salmon are all important resources used by terrestrial vertebrates. Cederholm et al. (2000) reported that 130 species of terrestrial vertebrates native to Washington and Oregon benefit (or historically benefited) from salmon and 80 of these species regularly utilize salmon. Salmon are consumed by a wide variety of terrestrial wildlife including waterfowl (Wood 1987a,b), gulls (Mossman 1958), corvids (Stalmaster and Gessman 1984), raptors (Stalmaster 1980, Stalmaster and Gessman 1984, Hansen 1987, Hunt et al. 1992), rodents (Lampman 1947), mustelids (Stenson et al. 1984, Dolhoff 1993, Ben-David et al. 1997a,b), canids (Szepanski et al. 1999), and ursids (Hilderbrand et al. 1996, Jacoby et al. 1999, Hilderbrand et al. 1999b,c).

Nutritional importance of salmon to wildlife

To simply note that salmon are consumed by wildlife greatly understates their ecological significance. Salmon tend to be a predictable, dependable, concentrated, and accessible resource high in protein and energy (Mathisen et al.1988). In addition, salmon are available at ecologically important time periods for various consumers. Juvenile salmon are consumed extensively by merganser (*Mergus merganser*) broods (contributing 80% of body mass at 10 days of age to 40% of body mass at 40 days of age) inhabiting streams in coastal British Columbia (Wood 1987b). Some raptor populations are believed to be energetically constrained in winter, and salmon can be the major food resource during this time of nutritional stress (Stalmaster and Gessman 1984). Ben-David (1997) reported that timing of reproduction, particularly lactation, in female mink (*Mustela vison*) in southeast Alaska deviated from the species norm and coincided with the availability of salmon carcasses. In years of low rodent numbers, salmon carcasses were a major component of the autumn diet of martens (*Martes americana*) in southeast Alaska (Ben-David et al. 1997a). Furthermore, body masses of martens consuming marine (salmon) diets did not differ from those eating terrestrial diets, suggesting that salmon carcass consumption allows body mass to be maintained in years of low primary prey availability (Ben-David et al. 1997a). On the Kenai Peninsula, Alaska, spawning adult salmon and salmon carcasses are the single most important fall resource to brown bears (*Ursus arctos*) as they accumulate energy reserves necessary to meet the demands of hibernation and cub production (Farley and Robbins 1995; Hilderbrand et al. 1999b, 2000).

Salmon and wildlife population productivity

A fundamental trait of any wildlife population and one central to wildlife conservation is population status

Table 1. Energy content (kcal) of king (*Oncorhynchus tshawytscha*), sockeye (*O. nerka*) and pink (*O. gorbuscha*) salmon collected during 1997 spawning migrations on the Kenai Peninsula, Alaska. Energy content was calculated as the product of the mass of individual salmon and the energy content of a homogenized sample combined across individuals determined by bomb calorimetry.

Type	Energy content, kcal (SD)					
	King	*n*	Sockeye	*n*	Pink	*n*
Fresh						
Whole male	—		5,620 (1,496)	5	3,034 (1,106)	6
Whole female	—		4,837 (1,218)	5	3,379 (228)	4
Roe	—		1,096 (448)	5	850 (248)	4
Ripe						
Whole male	5,760 (1,984)	5	5,348 (1,162)	5	2,433 (302)	5
Whole female	10,776 (1,138)	5	5,468 (397)	5	2,335 (467)	5
Roe	6,213 (687)	5	1,916 (430)	5	810 (141)	5
Spawned						
Whole male	8,874 (2,018)	3	4,937 (1,229)	5	1,835 (634)	6
Whole female	7,488 (1,357)	5	2,150 (250)	10	1,806 (471)	4

(i.e., how many are there, and is the population increasing or decreasing?). Despite the known importance of salmon, only 2 studies have illustrated direct relationships between salmon consumption and consumer population productivity. Bald eagles (*Haliaeetus leucocephalus*) in southeast Alaska had an increased proportion of active nests and an earlier laying date when salmon carcasses were abundant and available due to strong fall runs and a subsequent early spring thaw of spawning streams (Hansen 1987). Hilderbrand et al. (1999a) reported that mean adult female body mass, mean litter size, and density of brown bear populations all increased with increasing salmon consumption across North America.

Behavioral and evolutionary interactions

Several interesting behavioral and evolutionary relationships characterize the wildlife–salmon interaction and further emphasize its importance. Although salmon as a whole can be a valuable nutritional resource to wildlife, their nutritional value varies with life-stage and with body part (Mathisen et al. 1988, Tables 1 and 2). Mossman (1958) reported that glaucous-winged gulls (*Larus glaucescens*) kill and eviscerate more females than males, likely due to the high lipid content of the roe. Gende et al. (2001) report that bears feed selectively on energy-rich salmon parts and target individuals that had not yet spawned when salmon are abundant. Quinn and Kinnison (1999) report that brown bears on the Alaska Peninsula preferentially killed males vs. females and larger vs. smaller individuals. Ruggerone et al. (2000) reported similar findings for brown bears at a different study site on the Alaska Peninsula, and Reimchen (2000)

found the same trends held true for American black bears (*U. americanus*) consuming salmon in southeast Alaska. These studies illustrate the close link between salmon and consumer needed to drive the evolution of this type of behavior, as well as the sheer availability and abundance of the resource that allows for selective feeding. Furthermore, 3 studies (Quinn and Kinninson 1999, Reimchen 2000, Ruggerone et al. 2000) also argued that bear predation exerts sufficient selective pressure on salmon to affect phenotypic traits of salmon such as body size and shape. The fact that salmon consumers may be a significant selective force on salmon again illustrates the tight link between wildlife and salmon.

Behavioral interactions within and across species consuming salmon are also significant because the presence of salmon in streams does not necessarily mean that all species or individuals have equal access to the salmon resource. The literature is fraught with examples of one animal defending, stealing, or sharing a nutritional resource with other animals, and examples of interactions surrounding salmon are included in this body of behavioral observations (e.g. Stalmaster and Gessman 1984). However, this type of interaction may extend across populations and thus be of major ecological significance. Jacoby et al. (1999) reported that black bears on the Kenai Peninsula, Alaska, used salmon extensively in areas where brown bears did not occur (salmon comprised 53% [SD = 28%] of the black bears' diet). However, in areas where brown and black bears were sympatric, black bears did not use salmon at all. Access to salmon can vary greatly across individuals within a species as well. Farley et al. (2001) found that

Table 2. Energy contents (kcal/g fresh weight) of whole salmon and salmon body parts of king, sockeye, and pink salmon collected during 1997 spawning migrations on the Kenai Peninsula, Alaska. Values are means for species and spawning class. Energy content was compared using ANOVA ($F = 48.95$; $df = 4,29$; $P < 0.001$) and Tukey tests (Zar 1999).

Body part	Energy content, kcal (SD)	Tukey test
Whole male	1.38 (0.22)	a
Whole female	1.59 (0.25)	a
Roe	3.66 (0.32)	b
Skin	1.65 (0.53)	a
Heads	1.33 (0.33)	a

stream access by brown bears on the Kenai Peninsula, Alaska, varied temporally across reproductive classes, with lone females generally gaining access to salmon streams prior to females with yearlings, and females with cubs of the year tending to access streams after all other classes.

Ecological role of wildlife

Recent research suggests that wildlife may play an important role in nutrient cycling as a vector of nutrient redistribution. Ben-David et al. (1998a) reported that the movement of salmon carcasses out of the stream and into the riparian area occurred both by flooding and by predator activity and was reflected in the signatures of riparian vegetation. Furthermore, this increase in marine-derived nitrogen in riparian vegetation could be traced into local herbivores. Ben-David et al. (1998b) found increased levels of marine-derived nitrogen at river otter (*Lontra canadensis*) latrine sites relative to non-latrine sites in southeast Alaska. Thus, excretion of marine-derived nitrogen from salmon consumption may also be an important transport mechanism. This is supported by the work of Hilderbrand et al. (1999a) on the role of brown bears in the flow of marine nitrogen into a terrestrial ecosystem. In the fall, brown bears consume large quantities of salmon (>1000 kg, Hilderbrand et al. 1999b); however, the majority of the nitrogen is not assimilated because bears are selectively accumulating lipids. Hilderbrand et al. (1999a) estimated that the average female brown bear annually deposited 37.3 kg (SE=2.9 kg) of marine-derived nitrogen in the terrestrial ecosystem of the Kenai Peninsula, Alaska. The patterns of stream use by brown bears were closely correlated with trends of marine-derived nitrogen in vegetation seen at streams where salmon and brown bears both occurred.

This was not the case at streams that lacked salmon or streams that had salmon but where bears were largely excluded by human activity (Hilderbrand et al. 1999a).

The impact of salmon consumers on nutrient cycling likely extends beyond the terrestrial ecosystem and into the freshwater ecosystem in several ways. First, some salmon-derived nutrients are directly excreted back into the freshwater ecosystem. Second, Wipfli (1997) reported that terrestrial invertebrates were an important food source, comprising 38 and 57% of the diet of salmonids in old-growth and young-growth habitats, respectively. Because riparian vegetation productivity can have strong influences on stream food webs (as the source of terrestrial invertebrates, Wipfli [1997]), nutrient deposition in the riparian area by wildlife may directly benefit salmon productivity. Third, trees and vegetation growing in riparian areas eventually die, fall, and decompose. Thus, a portion of the marine nutrients deposited by consumers and taken up by and stored in terrestrial vegetation are ultimately recycled back into the freshwater ecosystem (Maser et al. 1988). Finally, productive salmon freshwater habitats are characterized by large organic debris and fallen trees that greatly influence the physiognomy and biology of streams (Sedell et al. 1988). Thus, increased productivity of riparian vegetation due to fertilization by terrestrial consumer activity ultimately enhances salmon habitat by increasing organic inputs and the physical diversity of the stream.

Human impacts on salmon–wildlife interactions

Humans can affect the wildlife–salmon interaction in 2 major ways: (1) by changing the availability of salmon, and (2) by changing the accessibility of salmon. Although human activities may increase the availability of or access to salmon by wildlife (e.g., stocking programs, beaver [*Castor canadensis*] dam removal, management), many human activities reduce the effectiveness of salmon as a nutritional resource to wildlife and thus may alter the complex ecological interactions discussed above as well as the productivity of wildlife populations.

Availability of salmon. In much of its historic range, salmon are still heavily used as a resource through sport-fishing, commercial fishing, and subsistence harvest. Salmon management in portions of the species range where salmon are harvested typically uses escapement targets that support maximum sustained yield. This tends to dampen the variation in annual salmon returns and, after escapement goals are met, results in a portion (the yield) of the salmon being harvested prior to their arrival at their spawning grounds.

This does not necessarily mean that in any given year fewer fish reach the spawning grounds than would in the absence of management. But obviously, any salmon harvested by humans is not available for consumption by wildlife, and wildlife and ecosystem requirements are not typically considered as part of escapement goals.

Commercial and sport fishing, logging, mining, agriculture, hydroelectric dams, and development have collectively reduced anadromous fish populations and adversely impacted ecosystems in Washington, Oregon, California, and Idaho (Nehlson et al. 1991, National Research Council 1996, Stouder et al. 1997, Cederholm et al. 2000, Gresh et al. 2000). In the mainstream Columbia and Snake rivers, more than 90% of the spawning habitat upstream of the Bonneville Dam has been inundated and can only be recovered through dam removal (Michael 1999), and nutrients delivered to freshwater ecosystems have been reduced to 6–7% of historic levels in Washington, Oregon, Idaho, and California (Gresh et al. 2000). Brown bears that inhabited the Columbia River drainage prior to hydroelectric development on the watershed relied heavily on salmon (58% [SD = 23%] of assimilated diet; Hilderbrand et al. 1996). Presently, few if any brown bears occupy these regions, and recovery of brown bear populations in this region would be greatly benefited by salmon recovery. Larkin and Slaney (1997) argue that while hatchery and stocking programs result in large volumes of returning marine nutrients, the influx of these nutrients may be focused in a few large streams and thus encourage oligotrophication of small, wild salmon streams. Thus, from an ecosystem recovery perspective, salmon recovery would preferably occur through dam removal rather than hatchery and stocking programs alone.

Access to salmon. Although the potential effects on wildlife of human activities that reduce the number of fish in the stream are easy to envision, a second potential impact of humans is the reduction in access to salmon by wildlife. Sport-fishing, wildlife viewing, and development on streams all may reduce the number of fish that can be used by wildlife if the wildlife are effectively excluded from fishing sites or avoid those areas due to a behavioral response to the presence of humans. Skagen et al. (1991) found that eagle consumption of salmon was reduced ten-fold on days when the eagles were disturbed by humans. Olson et al. (1997) report that non-habituated brown bears at Brooks River, Alaska, delayed their use of salmon streams by 17 days in 1992, apparently due to the presence of humans during an extended visitor season. Additionally, Olson et al. (1998) found that the presence of humans also affected the daily patterns of stream use by brown bears on the Alaska Peninsula. On streams with little or no human use, bears used the stream throughout the day. However, on a nearby stream with high levels of human use, brown bears tended to be crepuscular in their stream use.

Needed research
Quantification of salmon requirements of wildlife

To successfully manage any wildlife population, managers need to know what individuals and populations need to survive, reproduce, and recruit young into the population. Although salmon are consumed by >100 species of terrestrial vertebrates and are of ecological importance to many (see above), scientific estimates of the requirements of wildlife populations have rarely been attempted. Stalmaster and Gessman (1984) modeled energy requirements of wild, overwintering bald eagles in northwest Washington through a combination of wild and captive studies. Based on laboratory studies of metabolic requirements, food consumption, and critical temperatures in addition to activity budgets of wild eagles and typical ambient conditions of their environment, Stalmaster and Gessman (1984) estimated that daily salmon consumption by individual eagles was 489 g. Hilderbrand et al. (1999c) assessed the seasonal diets and changes in body composition of adult female brown bears on the Kenai Peninsula, Alaska. Salmon accounted for 59.6% (SD = 35.3) of the assimilated diet of bears after salmon arrival. Between salmon arrival and den entry, adult female brown bears gained 65.1 kg (SD = 24.1 kg), and these gains were primarily comprised of lipids 81.0% (SD = 19.6%). This information, coupled with captive feeding trials that established relationships between salmon intake and lipid and protein gains, allowed Hilderbrand et al. (1999c) to estimate annual salmon consumption of individual adult female brown bears at 1,003 kg (SD = 489 kg). Although both of the above studies provide sound estimates of salmon consumption by wildlife, they are only a first step because they provide data for only 1 season (Stalmaster and Gessman 1984) or 1 segment of the population (Hilderbrand et al. 1999c). In addition, consumption rates of individuals must be combined with sound estimates of population size and structure to develop estimates of salmon requirements for an entire wildlife population.

As an example, we combine data from 3 brown bear studies in 3 areas to derive a salmon escapement goal for a hypothetical bear population. This example is illustrative and is not a recommendation for any real population.

Further, we use published data of other authors, but we are not suggesting that their data be used in practice for such a purpose without their involvement and insights.

Gende et al. (2001) investigated selective feeding by brown bears in Bristol Bay and southeastern Alaska. The degree of selective feeding was related to salmon availability, because selectivity, largely for high energy parts, increased with increasing salmon density. For our sample calculations, we assume that 55.5% of each salmon is consumed. This is the proportion consumed per fish at a density of 0.5 salmon/m^2 in small ponds and streams in the Pedro Pond system (Gende et al. 2001:Fig. 3b). We also assume that 91.9% of the salmon consumed are ripe and thus do not spawn due to consumption. We calculated this value from the number of ripe and spawned-out fish consumed by bears and the proportion at which they were consumed (Gende et al. 2001:Table 4).

Hilderbrand et al. (1999*b*) combined stable isotope analysis of diet with changes in body composition to estimate annual salmon consumption rates of individual brown bears on the Kenai Peninsula, Alaska, at 1,003 kg (SD = 487 kg). This estimate did not reflect selective feeding by brown bears; consumption of roe alone (i.e., complete selective feeding) would reduce this estimate by 58%. Because some selective feeding certainly occurs (see Gende et al. 2001, discussed above), we are likely overestimating the biomass of salmon consumed by female brown bears. However, our estimate for females likely underestimates salmon consumption by males due to their larger body size and social dominance. For this exercise, we use 1,003 kg/bear/year (Hilderbrand et al. 1999*b*) as the average requirement for all bears.

Mowat and Strobeck (2000) utilized microsatellite DNA markers in combination with mark–recapture models to estimate the size of a grizzly bear population in a 9,866 km^2 area in southeast British Columbia. The population size was estimated to be 262 (95% CI = 224–313) bears.

Using data from these 3 studies as parameters for our hypothetical bear population yields an estimate of annual salmon consumption of:

$$(262 \text{ bears})(1,003 \text{ kg salmon consumed/bear/year})$$
$$= 2.63 \times 10^5 \text{ kg salmon consumed/year}$$

Using the average size of ripe female Kenai sockeye salmon of 3.72 kg (SD = 0.27 kg) (Hilderbrand, unpublished data), the number of salmon consumed by this hypothetical population would be:

$$(2.63 \times 10^5 \text{ kg/year})/(3.72 \text{ kg/salmon})$$
$$= 7.06 \times 10^4 \text{ salmon/year}$$

However, due to selective choice by brown bears, we assume that only 55% of each fish is consumed, thus the estimate must be corrected as follows:

$$(7.06 \times 10^4 \text{ salmon/year})/(0.55)$$
$$= 1.28 \times 10^5 \text{ salmon/year}$$

Finally, this estimate would be slightly reduced because 8.1% of the salmon consumption is of spawned-out carcasses. These fish have already reproduced and would be part of base allocations. The salmon requirement of this hypothetical bear population would be:

$$(1.28 \times 10^5 \text{ salmon/year})(0.919)$$
$$= 1.18 \times 10^5 \text{ salmon/year}$$

Thus, to meet the needs of this hypothetical bear population, an additional 118,000 salmon would need to be added to current base escapement goals. These 118,000 salmon represent the number of salmon that must be captured to meet population requirements. Consumers are not 100% efficient at capturing all available salmon; thus, this estimate is a minimum.

In practice, the development of salmon allocations for wildlife would be a process involving wildlife and fisheries managers as well as other interested parties. Site-specific data would be required, and further information and data analysis (bear population sex ratio and age structure, measure of variation around the estimate, temporal feeding patterns) would strengthen these estimates and the ecological soundness of their application. Techniques are available to estimate the parameters necessary to develop sound estimates of salmon requirements of wildlife populations. Due to the import of salmon to wildlife and ecosystems, development of these wildlife allocations should be implemented for wildlife populations for which conservation is an issue.

Conclusions

Coastal ecosystems are particularly complex because of the movement of elements, nutrients, individuals, and species across traditionally defined ecosystem boundaries. This complexity calls for integrated management with a perspective beyond the recovery or harvest of individual species (Stouder et al. 1997, Cederholm et al. 2000). Bilby et al. (2001) have proposed using the relationship between carcass abundance in the fall and

stable nitrogen isotope values in coho parr late the following winter to supplement traditional methods of establishing escapement goals. This approach acknowledges the importance of salmon-derived nutrients to the freshwater ecosystem by looking for marine nitrogen saturation levels within the system, using coho parr as an indicator. We commend this approach, as it incorporates ecosystem level processes and nutrient levels. However, as it focuses on in-stream nitrogen levels, it does not fully bridge the gap between the aquatic and terrestrial ecosystems. We believe salmon and wildlife must be viewed as integral components of the same system (Willson and Halupka 1995, Willson et al. 1998, Hilderbrand et al. 1999*a*, Cederholm et al. 2000). Salmon management should account for the requirements of wildlife (i.e., salmon should be allocated to wildlife) (Hilderbrand et al. 1999*a,c*) and the role of wildlife in ecosystem level processes should be considered when managing habitat, wildlife, and human activities (Hilderbrand et al. 1999*a*). Stalmaster and Gessman (1984) and Hilderbrand et al. (1999*c*) have estimated salmon consumption by individual eagles and brown bears, respectively. Coupled with sound population estimates, these values can provide minimum species requirements than can be added to escapement goals. Further data on selective feeding, timing of salmon consumption (pre- or post-spawning), and capture efficiency can further refine these estimates. To this end, population estimation and salmon foraging studies are currently being conducted for brown bears on the Kenai Peninsula, Alaska.

Whether the goal is salmon recovery (e.g., Columbia River salmon) or sustainable salmon harvest (Alaska), sound management requires a basic understanding of the nutrient dynamics of ecosystems, the salmon requirements of wildlife species, the ecological role played by wildlife in the productivity of both the terrestrial and freshwater ecosystems, and the potential impacts of human activities on ecosystem function. Only through broad-perspective, integrated management can our coastal ecosystems as a whole, and thus our individual resources, be best conserved and used in perpetuity.

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